University of Alberta

The fungal communities of decomposing plants in southern boreal peatlands of Alberta, Canada

by

Markus Norbert Thormann ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Doctor of Philosophy*

in

Environmental Biology and Ecology

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Für meinen Papa Wolfgang und meinen Großeltern, Opa Heinz, Opa Henner, und Oma Paula, ich wünschte ihr wärt hier und könntet dies mit mir erleben, und meinen Eltern und Verwandten in Kanada und Deutschland.

Vielen Dank für Eure Hilfe und Eurem Glauben an mich über die vergangenen Jahre.

Abstract

Peatlands are some of the world's most important ecosystems, primarily because they cover a large area of the world and store large quantities of carbon in peat. Under a global warming scenario, this peat is predicted to decompose more rapidly than at currant rates, thereby releasing increasing quantities of CO_2 and/or CH_4 into the atmosphere, providing a positive feedback to global warming. Therefore, it is important to understand current decomposition dynamics of plant litters in peatlands and gain an understanding of the microbial communities involved in the decomposition of these materials.

In a decomposition study of above- and belowground plant litters in a fen and a bog in southern boreal Alberta, mass losses of *Carex aquatilis* rhizomes significantly exceeded those of *C. aquatilis* leaves, *Salix planifolia* leaves, *S. planifolia* roots, and *Sphagnum fuscum* after two years. Tissue nutrient concentrations and alkalinity- and phosphorus-related surface water chemistry variables explained most of the variation observed in these mass losses. Over 90 different fungal species were isolated from these plant litters. Community analyses showed that significantly different fungal communities (mycotas) were involved in the decomposition of these litters, with clear separations among the mycotas of the root, rhizome, and bryophyte litters. The mycotas of the leaf litters were similar to each other. Furthermore, distinct successional patterns of the mycota were apparent in the *S. fuscum* and *C. aquatilis* leaf and rhizome litters. Contrary to the literature, litter quality variables accounted for most of the underlying trends, with environmental variables playing only a minor role.

A comparative *in vitro* analysis of fungal and bacterial decomposition of *Sphagnum fuscum* and *Carex aquatilis* leaves and rhizomes at two temperatures showed that fungi caused greater mass losses at elevated temperatures (6 °C temperature increase), similar to those predicted under a global warming scenario. Mass losses of *S. fuscum* by bacteria were significantly greater than those by fungi at current mean growing season temperatures. These

data suggest that increased decomposition rates of peat in peatlands as predicted by current ecosystem climate models may be premature and simplistic.

Nutrients released into the soil and water columns during the process of decomposition are then available for plant uptake. Mycorrhizal fungi associated with roots of most bog and fen plant species (Ericaceae, Pinaceae, Salicaceae) facilitate the acquisition of these nutrients and ensure plant vigor and survival. In contrast, plants belonging to the Cyperaceae and Typhaceae in fens and marshes were non-mycorrhizal, but had a suite of often dark-coloured, septate fungi associated with their roots. These may act like mycorrhizal fungi in some instances, aiding plants in the acquisition of nutrients.

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First I would like to express gratitude to my supervisors, Drs. Suzanne Bayley and Randy Currah. I will always be indebted to them for their guidance, support, and patience with me. Suzanne, you always took time to discuss even the smallest aspects of my research, even when you were swamped with work yourself. You took a chance with me at the beginning of my post-graduate career and guided me not just through my M.Sc. but also my Ph.D. research. I am grateful for your faith in me. Randy, I thank you for introducing me to the wonders of mycology, I now appreciate fungi to be the true "movers and shakers" out there. Both of you made my stay in your labs a pleasure and something I will cherish forever.

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List of Abbreviations and Symbols

Chemical Terms and Abbreviations

Alk. - Alkalinity

C - Carbon

Ca^{2+} - Calcium ion

CH_4 - Methane

CO_2 - Carbon dioxide

C:N - Carbon to nitrogen ratio

Cond. - Conductivity

HCO_3^- - Bicarbonate ion

K^+ - Potassium ion

N - Nitrogen

NH_4NO_3 - Ammonium nitrate

NH_4^+ - Ammonium ion

NO_3^- - Nitrate ion

NO_X - Nitrous oxide

P - Phosphorus

SRP - Soluble reactive phosphorus

TC:TN - Total carbon to total nitrogen ratio

TDP - Total dissolved phosphorus

TN - Total nitrogen

TP - Total phosphorus

d-$H_2$0 - Distilled water

Ecological Measurement Terms and Abbreviations

NPP - Net primary production

X - Final weight

X_0 - Initial weight

Fungal and Bacterial Growth Media

AG - Agarose gel

MEA - Malt extract agar

MMN - Modified Melin-Norkrans medium
MYC - Mycobiotic agar
MYEA - Malt yeast extract agar
PCA - Plate count agar
PBA - Peptone broth agar
PDA - Potato dextrose agar

Herbaria Abbreviations

ALTA - University of Alberta Cryptogamic Herbarium
CBS - Centraalbureau voor Schimmelcultures
NoF - Northern Forestry Centre
UAMH - University of Alberta Microfungus Collection and Herbarium

Measurements

cm - Centimeter
°C - Degrees Celsius
g - Gram
L - Liter
m - Meter
mg - Milligram (1×10^{-3} g = 0.001 g)
min - Minute(s)
mL - Milliliter (1×10^{-3} L = 0.001 L)
mM - milli Molar (concentration)
Pg - Petagram (1×10^{15} g)
t - Time
μg - Microgram (1×10^{-6} g = 0.000001 g)
μS - Micro Siemens
$v\ v^{-1}$ - Volume per volume
$w\ v^{-1}$ - Weight per volume

Molecular Techniques and Terminology

IGS - Intergenic spacer region
PCR - Polymerase chain reaction
RFLP - Restriction fragment length polymorphism

Mycological Terms and Abbreviations

EM - Ectomycorrhizal
MRA - *Mycelium radicis atrovirens*
NABS - North American Biological Species
PPO - Polyphenol oxidases
VA-mycorrhizal - Vesicular-arbuscular mycorrhizal

Site Abbreviation

RSF - Riverine sedge fen

Statistical Terms and Abbreviations

a - y-intercept of a regression line
ANOVA - Analysis of variance
arith - Arithmetic
b - Slope of a regression line
corr. - Correlation
log - Logarithm, logarithmic
n - Sample size
n.d. - Not determined
n.s. - Not significant ($p > 0.05$)
p - Probability
r - Correlation coefficient
r^2 - Coefficient of determination
x - Independent variable
y - Dependent variable

Symbols

$>$ - Greater than
$\geq$ - Greater than or equal
$<$ - Less than
$\leq$ - Less than or equal

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CHAPTER 1. INTRODUCTION

Peatlands

Peatlands cover approximately 4% of the world's, 14% of Canada's (National Wetlands Working Group 1988), and 16% of Alberta's landscape (Vitt et al. 1996). Specifically, Alberta's landscape consists of approximately 4.9% bogs and 11.4% fens (Vitt et al. 1996). Northern bogs are ombrotrophic ecosystems that receive water and nutrients solely from precipitation. These bogs are dominated by species of *Sphagnum*, *Picea mariana* (Mill.) BSP., and members of the Ericaceae, including species of *Rhododendron*, *Andromeda*, and *Vaccinium*. Conversely, fens are minerotrophic ecosystems that receive water and nutrients from precipitation and ground and/or surface water flow. Fens can be subdivided into poor and rich fens. Poor fens are characterized by low mineral ion concentrations in the surface water and few moss indicator species, most of which are species of *Sphagnum* (Vitt 1994). In contrast, rich fens are characterized by high mineral concentrations in the surface water and an increasing number of moss indicator species, such as species of *Drepanocladus*, *Scorpidium*, and *Aulacomnium* ("brown" mosses) (Vitt 1994). Additionally, shrubs, such as species of *Salix* and *Betula*, and herbaceous plants, such as species of *Carex*, are found in poor fen and rich fens. Although pH and alkalinity-related variables and water levels are significantly lower in bogs than fens, surface water concentrations of nitrogen (N) and phosphorus (P) are similar between these two types of peatlands (Vitt 1994, Szumigalski and Bayley 1996, Thormann and Bayley 1997, Thormann et al. 2001).

Halsey et al. (2000) and Vitt et al. (2000) estimated that continental western North American peatlands (Alberta, Saskatchewan, and Manitoba) developed and began accumulating carbon (C) approximately 9,000 years ago. Since then, they have accumulated approximately 9.95×10^{13} g C yr^{-1}, totaling an estimated 48.0 Pg of C (Pg = Petagram, 1 Pg = 1×10^{15} g), or 2.1% of the world's terrestrial C in 0.25% of the world's landbase (Vitt et al. 2000). Global climate models (GCM) predict increasing atmospheric temperatures of 3-10 °C under a 2 x CO_2 scenario, with greater temperature increases at higher latitudes (Boer et al. 1992). These temperature increases have been predicted to cause a change in the sink/source balance of peatlands. Therefore, these ecosystems, currently long-term greenhouse gas sinks (Bellisario et al. 1998, Vitt et al. 2000), may become significant sources of greenhouse gases, such as methane (CH_4) and carbon dioxide (CO_2), providing a positive feedback to global warming (Gorham 1991, Hogg et al. 1992, Moore and Dalva 1993).

Decomposition dynamics

Peatlands accumulate C annually (Thormann et al. 1999) due to an imbalance between plant net primary production and decomposition (Clymo 1965, Malmer 1986, Farrish and Grigal 1988, Vitt 1990). Decomposition is a complex process that includes nearly all changes in organic matter that has undergone senescence or death (Brinson et al. 1981). Leaching of soluble organic matter precedes losses due to assimilation by microorganisms or removal by animals. Decomposition is completed with the loss of the physical structure and changes in the chemical constituents of the remaining organic matter (Clymo 1983). The most common method to assess rates of decomposition involves measuring the rate of mass loss of a known quantity of litter over time. The rate of plant decomposition is affected by moisture, oxygen availability, temperature, acidity, and the nutrient status of ecosystems (primarily N- and P-related surface water chemistry variables) (Brinson et al. 1981, Bartsch and Moore 1985, Farrish and Grigal 1988, Gorham 1991, Szumigalski and Bayley 1996, Thormann and Bayley 1997). Although litter quality also affects the rate of decomposition (Brinson et al. 1981, Bridgham and Richardson 1992, Szumigalski and Bayley 1996), Thormann et al. (1999) suggested that water levels might be more important than surface water chemical and/or litter quality variables in affecting decomposition of plant litter under aerobic conditions in peatlands.

Fungi

Fungal communities play an important role in ecosystems by transforming and translocating nutrients (Harley and Smith 1983). Nutrients, such as N and P, leach from plants during the early stages of decomposition, and fungi and bacteria further degrade plant litter after senescence and death of the plant during the later stages of decomposition (Mitsch and Gosselink 2000). Fungi synthesize a variety of enzymes, such as cellulases, amylases, and pectinases, that facilitate the decomposition of most plant materials (Domsch et al. 1980). Freeman et al. (2001) suggested that the only variable limiting the degradation of phenolics-rich peat at present are anoxic conditions throughout most of the peat profile, thereby limiting the activity of polyphenol oxidases (PPO), the enzymes required for the degradation of the most complex plant structural polymers (lignins, tannins, and their derivatives). However, this theory is simplistic in that the ability of fungi to synthesize PPOs is limited (Domsch et al. 1980), because a suite of enzymes is required to degrade these substrata, rather than a single enzyme, such as cellulases for the degradation for cellulose.

A succession of fungi during the process of decomposition ("litter succession") has been observed in a variety of plant species in terrestrial (Frankland 1966, Saitô 1966, Kasai et al. 1995, Lumley et al. 2001) and wetland (Pugh 1958, Pugh and Mulder 1971, Apinis et al. 1972, Cabral et al. 1993, Tokumasu 1994) ecosystems. Litter succession of saprobes has been linked to changes in litter quality, water potential of the litter, temperature, pH, and seasonality (Pugh 1958, Christensen and Whittingham 1965, Pugh and Mulder 1971, Dix 1985, Nilsson et al. 1992, Lumley et al. 2001). However, in contrast to succession in plant communities, terminating in a climax community, succession of saprobes results in the decomposition of organic substrates and a climax community does not result. Ultimately, nutrients are released during the decay of organic matter. These are then available for future plant growth.

Mycorrhizas are mostly mutualistic associations between fungi and the roots of higher plants, in which the fungi form consistently recognizable and physically distinct associations without causing any perceivable negative effect (Fernando 1995). There are four major types of mycorrhizas (Smith and Read 1997): (1) ectomycorrhizas, common to most woody plant species; (2) vesicular-arbuscular mycorrhizas (VAM), common to most herbaceous plant species; (3) ericoid mycorrhizas, common in members of the Ericales; and (4) orchid mycorrhizas, limited to orchids. Mycorrhizas are common in most ecosystems and their presence suggests that they play ecologically significant roles (Wetzel and van der Valk 1996, Näsholm et al. 1998, van der Heijden et al. 1998). These fungi assist in the acquisition, storage, and translocation of nutrients, thereby facilitating the establishment and vigor of many plant species. Their significance has been shown in many stressed ecosystems, including high altitude (Haselwandter and Read 1982), high latitude (Kohn and Stasovski 1990), and nutrient-limited ecosystems (Haselwandter 1987).

Thesis objectives

The main purpose of this study was to determine the microfungal communities (mycota), throughout the process of decomposition, of the dominant peat-forming plant species of a southern boreal bog and fen in Alberta, Canada. The major hypothesis was that the mycota of the dominant fen and bog vegetation differs at different stages of decomposition and that they are a reflection of the litter quality, surface water chemistry, and physical variables that define these two types of peatlands and their vegetation. These plant species and their tissues were *Sphagnum fuscum* (Schimp.) Klinggr. from a bog and *Carex aquatilis* Wahlenb. leaves and rhizomes and *Salix planifolia* Pursh leaves and roots from a riverine fen.

Chapter 2 describes mass losses of these plant litters and examines the influence of various litter quality, surface water chemistry, and physical variables on the decomposition dynamics. I hypothesized that (1) *Carex aquatilis* rhizomes will decompose faster than *C. aquatilis* leaves, *Salix* planifolia leaves and *S. planifolia* roots in a fen, and *Sphagnum fuscum* in a bog, because rhizomes are nutrient-storage tissues of the plant and thus may have higher concentrations of total nitrogen and total phosphorus and (2) *S. planifolia* roots will decompose more slowly than all other litter types across all species as a result of their woody tissues, which may be more resistant to decomposition than herbaceous tissues.

Throughout the two-year decomposition period, sub-samples of the five decomposing plant litters from both peatlands were used to isolate filamentous microfungi. Chapter 3 provides brief annotations of all fungal species identified and/or described during this endeavor. These annotations include distinguishing colonial and/or morphological characters, information on the distribution, source of isolates, and enzymatic capabilities of each fungal species.

The primary objective of Chapter 4 was to examine differences in the mycota of the dominant bog and fen plant species and to determine the influence of environmental variables on their mycotas. Furthermore, I wanted to determine if clear patterns of fungal succession were apparent during the process of decomposition of each litter type. I hypothesized that (1) the mycota of the dominant bog and fen plant species differs significantly and (2) distinct fungal successional patterns emerge during the decomposition of each of these litter types. Differences in the mycota and distinct successional patterns were expected because of different total carbon (TC), total nitrogen (TN), and total phosphorus (TP) tissue nutrient concentrations and TC:TN quotients of these plant tissues and significantly different pH and alkalinity-related variables and water levels between bogs and fens. Furthermore, many fungi are highly substrate-specific and may only occur at certain stages of decomposition of the three plant litters.

Chapter 5 presents data on comparative mass losses of *Sphagnum fuscum* and *Carex aquatilis* leaves and rhizomes caused by their respective dominant indigenous fungi and bacteria *in vitro*. This study also examines the effects of increasing temperatures, similar to those expected at northern latitudes under a global warming scenario. I hypothesized that (1) fungi will cause larger mass losses of these litter types than bacteria, because fungi have higher growth rates and therefore will be able to colonize the plant litters more effectively than bacteria, (2) mass losses caused by fungi and bacteria will increase with increasing temperatures, because their rates of growth and enzyme synthesis generally are optimal between 20 and 30 °C (mesophilic), although there are psychrophilic (growth optima below 10 °C) bacteria and fungi as well, (3) mass losses of the litter types will be greatest when bacterial and fungal populations coexist, because of synergistic relationships between these microbial populations, and (4) mass losses of the *Carex* litters will exceed those of the *Sphagnum* litter, because of higher initial concentrations of TN and TP in the fen plants.

Chapter 6 provides an account of the mycorrhizal status of the dominant plant species along a bog – fen – marsh wetland gradient in southern boreal Alberta. I hypothesized that (1) all plant species examined in bogs and fens will be mycorrhizal because taxonomically closely related species from non-peatland ecosystems have previously been shown to be mycorrhizal, (2) the ectomycorrhizal fungus *Cenococcum geophilum* Fr. will be present in roots of all woody plant species due to its circumboreal distribution, and (3) the dominant vegetation of marshes will be non-mycorrhizal, because both VAM and ectomycorrhizal fungi have been reported to decrease in occurrence in waterlogged soils.

The final chapter, chapter 7, summarizes the major results of this study and suggests future research directions.

During the course of this study, several peripheral projects were carried out that warrant inclusion in this thesis but not as individual thesis chapters. *Armillaria sinapina* Bérubé & Dessur., a common pathogen of western boreal forest trees, was isolated from living and decomposing herbaceous fen vegetation. Appendix 1 discusses the methods used to identify this fungus and some ecological aspects of its distribution in herbaceous plants of peatlands. Appendix 2 provides annotations of all fungi identified and/or described from living and decomposing *Sphagnum fuscum* from the bog in this study, while Appendix 3 discusses the enzymatic abilities and ecology of some of these fungi in light of their potential roles as mineralizers of peat. Appendix 4 shows collection and accession numbers of all fungi identified and/or described in this study. Appendix 5 is a glossary of mycological terms. Appendix 6 is the *curriculum vitae* of the author.

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CHAPTER 2. COMPARISON OF DECOMPOSITION OF BELOWGROUND AND ABOVEGROUND PLANT LITTERS IN PEATLANDS OF BOREAL ALBERTA, CANADA [1]

INTRODUCTION

Peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and 16% of Alberta's landbase (Vitt et al. 1996). Specifically, bogs cover approximately 4.9% and fens approximately 11.4% of Alberta's landbase (Vitt et al. 1996). These ecosystems are important to the global carbon cycle due to the accumulation of carbon in the form of peat (a heterogeneous assemblage of partially decomposed plant matter). Peat accumulates on an annual basis (Thormann et al. 1999a) and it has been suggested that peat accumulation is the result of slow rates of litter decomposition rather than high rates of net primary plant production (Clymo 1965, Malmer 1986, Farrish and Grigal 1988, Vitt 1990).

The rate of plant decomposition is affected by moisture, anoxia (acrotelm *vs.* catotelm), temperature, acidity, and the nutrient status of ecosystems (primarily nitrogen- and phosphorus-related water chemistry variables) (Brinson et al. 1981, Bartsch and Moore 1985, Farrish and Grigal 1988, Gorham 1991, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a). Although litter quality also affects the rate of decomposition (total nitrogen [TN], total phosphorus [TP], and total carbon [TC] tissue concentrations, TC:TN quotients) (Brinson et al. 1981, Bridgham and Richardson 1992, Szumigalski and Bayley 1996a), Thormann et al. (1999a) suggested that water levels might be more important than surface water chemical and/or litter quality variables in affecting decomposition of plant litter in peatlands.

Most decomposition studies of vascular and non-vascular plant litter in peatlands have concentrated on aboveground plant material (Clymo 1965, Reader and Stewart 1972, Chamie and Richardson 1978, Bartsch and Moore 1985, Ohlson 1987, Verhoeven and Arts 1992, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a, Arp et al. 1999). Decomposition rates of belowground tissues have been measured rarely in terrestrial ecosystems (McClaugherty et al. 1982, Robinson et al. 1999). In wetland ecosystems, the majority of these studies have been conducted in marshes (Puriveth 1980, Hackney and de la Cruz 1980, Buth 1987, Hemminga et al. 1988, Benner et al. 1991, Pozo and Colino 1992, Wrubleski et al. 1997) or anthropogenically manipulated wetlands (Hartmann 1999). To my knowledge, there are no decomposition studies of belowground plant litters in "natural" peatlands in North America and only one in Europe (Heal et al. 1978). This is surprising, because some studies have suggested that belowground production of some peatland plant species may account for up to 95% of the total production (Bernard and Fiala 1986, Wallén 1986, Backéus 1990, Saarinen 1996). Belowground production of sedges is primarily in the form of rhizomes and fibrous roots that may be long-lived, depending on the sedge species (Sjörs 1988). Similarly, belowground production of woody plant species, such as species of *Betula* and *Salix*, has not been determined in peatlands; however, it can account for up to 75% of the total net primary production in forest ecosystems (Persson 1978, Fogel 1983, Nadelhoffer and Raich 1992, Burke and Raynal 1994).

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[1] A version of this chapter has been published: Thormann, M. N., S. E. Bayley, and R. S. Currah. 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Canadian Journal of Botany **79**: 9-22.

The greatest decomposition rates occur in the aerobic soil horizon, the acrotelm (Clymo 1965). As peat accumulates, the lower peat profile becomes the anaerobic catotelm and decomposition rates decrease significantly due to the absence of oxygen for decomposer communities. Thormann et al. (1999a) measured short-term peat and carbon accumulation potentials along a bog-fen-marsh wetland gradient in Alberta, Canada. Their results indicate an increasing potential for carbon and peat accumulation from marshes to fens to bogs. However, they only examined the contribution of aboveground plant tissues and excluded the contribution of belowground plant tissues in their study, because of the scarcity of belowground plant production and decomposition data in the literature. It is useful to investigate the decay rates of the belowground plant tissues as well, due to their large contribution to the total plant production in most wetlands. Much of the belowground plant tissues is located in the catotelm and remains alive via the transportation of oxygen through aerenchyma tissues to roots and rhizomes (Fagersted 1992, Jackson and Armstrong 1999). However, roots and rhizomes, which may be perennial, turn over periodically, thereby contributing to peat and carbon accumulation in wetlands, similar to the contribution of annual aboveground plant tissues.

Because sedge- and shrub-dominated fens constitute approximately 35 and 34%, respectively, of all peatlands in Alberta (Vitt et al. 1996), the focus of this study was to determine mass losses of *Carex aquatilis* Wahlenb. rhizomes and *Salix planifolia* Pursh roots in an open, rich fen and compare them to mass losses of aboveground plant tissues of other peatland plant species. I hypothesized that (1) *C. aquatilis* rhizomes will decompose faster than *C. aquatilis* leaves, *S. planifolia* leaves and *S. planifolia* roots in a fen, and *Sphagnum fuscum* (Schimp.) Klinggr. in a bog, because rhizomes are nutrient-storage tissues of the plant and thus may have higher concentrations of total nitrogen and total phosphorus and (2) *S. planifolia* roots will decompose more slowly than all other litter types across all species as a result of their woody tissues which may be more resistant to decomposition than herbaceous tissues.

METHODS

Study areas and site descriptions

The riverine sedge fen and Perryvale bog lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). The area has mild summers and cold, snowy winters with a long-term mean annual temperature of 1.7 °C and a total mean annual precipitation of approximately 500 mm (Environment Canada 1982).

These sites have been described in detail in Thormann et al. (1999b). Briefly, the riverine sedge fen is dominated by *Carex aquatilis*, *Carex lasiocarpa* Ehrh., *Salix planifolia*, and *Equisetum fluviatile* L. The bryophyte stratum is sparse and discontinuous and consists primarily of *Brachythecium mildeanum* (Schimp.) Schimp. *ex* Milde and *Tomenthypnum nitens* (Hedw.) Loeske. The Perryvale bog is dominated by *Sphagnum fuscum*, *Sphagnum angustifolium* (C. Jens *ex* Russ.) C. Jens, *Picea mariana* (Mill.) BSP., and members of the Ericaceae, including *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Andromeda polifolia* L.

Decomposition measurements

The methods used to set up the decomposition experiment follow those in Thormann and Bayley (1997a). Briefly, live aerial and belowground portions of the dominant plant species from each site were collected in early September 1997. These were *Sphagnum fuscum* in the bog and *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots in the sedge fen. Only senesced leaf litters were collected (yellow to pale-brown in colour) and used in this study. *Carex aquatilis* rhizomes were extracted by cutting the peat with a knife in a 30 cm diameter circle around individual *C. aquatilis* plants. After these "cores" were carefully lifted, adhering peat and plant debris were washed free from the rhizomes with water from the fen. Rhizomes were separated from individual plants. Living *C. aquatilis* rhizomes (approximate diameter 3-5 mm) are firm and light-brown, in contrast to dead ones, which are soft and dark-brown to black.

Roots of *Salix planifolia* were collected from carefully extracted whole plants (< 1 m in height). The root material for this study was randomly selected from all roots with a diameter of approximately 2 mm or less. Of these, approximately half had secondary growth and was woody, while the remaining material lacked secondary growth and was non-woody (fine roots).

In the bog, the top 3 cm of living, healthy *Sphagnum fuscum* plants, including stems, branches, all associated leaves, and the capitulum, were collected for the decomposition study. All plant material was oven-dried to constant mass at 60 °C and 1.8-2.5 g randomly selected material from each litter type was placed in individual nylon mesh bags (3 x 6 cm, 1-mm mesh gauge). The filled bags were weighed to the nearest 0.001 g, sewn shut, and placed either horizontally 3-10 cm beneath (*S. fuscum*, *Salix planifolia* roots, and *Carex aquatilis* rhizomes) or on top of the peat surface (*C. aquatilis* and *S. planifolia* leaves) to mimic "natural" decomposition conditions. Buried bags were in the acrotelm in both sites but they were below the water level in the fen and above the water level in the bog. Decomposition bags with the individual litters were placed in the site of the origin of the litter, thus, fen litter decomposed only in the fen and bog litter decomposed only in the bog.

Twenty-four decomposition bags per litter type, each tied to a wooden stake to avoid losses, were deployed in mid-September 1997. Four decomposition bags from each litter type were retrieved from each site after 20 and 50 days (1997) and eight, 12 (1998), 20, and 24 months (1999). Bags were cleaned immediately by removing coarse, intruding roots and other debris, such as leaves of other vascular and non-vascular plants that had grown into or through the leaf litter decomposition bags. Finer debris (soil, remaining "alien" plant parts, fungal mycelium, etc…) was removed carefully in the laboratory with forceps before drying to constant mass at 60 °C. Each bag was then weighed, again to the nearest 0.001 g.

The percent masses remaining (MR) over the six incubation periods were determined using the following equation:

$$MR = \{(X_0 - X) / X_0\} \times 100$$

where X_0 represents the initial dry litter mass (g) before decomposition and X the final dry litter mass (g) after incubation in the field. The 20-month decomposition bag set of *Sphagnum fuscum* in the bog was disturbed by animals, but still was used for all subsequent analyses.

Environmental and litter quality variables

The litter quality was determined by analyzing dried and finely ground plant litter samples for TC and TN concentrations using a Model 440 Elemental Analyzer (Control Equipment Corp.). TP tissue concentrations were determined using the molybdophosphovanadate method with an Auto Analyzer as outlined by Prepas and Rigler

(1982) and Parkinson and Allen (1975). Water samples were collected monthly from a depression within the peat during the ice-free season (May-November) and analyzed for nitrate (NO_3^-), ammonium (NH_4^+), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP), pH, conductivity, alkalinity, bicarbonate (HCO_3^-), dissolved organic carbon (DOC), calcium (Ca^{2+}), and potassium (K^+). Furthermore, water levels were monitored monthly using meter sticks (attached to permanent wooden stakes driven into the mineral substrate) and the depth of the acrotelm was determined monthly using steel welding rods inserted into the peat as described by Bridgham et al. (1991). These techniques and analyses followed Thormann and Bayley (1997a).

Peat and carbon accumulation potentials of the five litters

I did not measure above- and belowground net primary production (NPP) of *Carex aquatilis* and *Salix planifolia* in the riverine sedge fen and *Sphagnum fuscum* in the bog in this study. Therefore, I adopted aboveground NPP values for *Salix* spp. (46 g m^{-2} yr^{-1}, mean of aboveground NPP values of *Salix* spp. in moderate-rich and rich fens) and *C. aquatilis* (409 g m^{-2} yr^{-1}) in the sedge fen from Thormann and Bayley (1997b). A NPP value of 190 g m^{-2} $year^{-1}$ was assumed for *S. fuscum* in the bog, which is the mean of NPP values reported by Thormann and Bayley (1997b) and Szumigalski and Bayley (1996b). Belowground NPP values for *C. aquatilis* and *S. planifolia* were estimated from Campbell et al. (2000) as 50% of the total NPP, thus, the total belowground NPP of *Carex aquatilis* in the riverine sedge fen was estimated at 409 g m^{-2} $year^{-1}$ and that of *S. planifolia* was estimated at 46 g m^{-2} $year^{-1}$. Using these values and the mass loss and TC tissue concentrations from this study, I calculated peat and carbon accumulation potentials of these five litter types after one and two years of decomposition.

Statistical analyses

Kruskal-Wallis tests (non-parametric, one-way analyses of variance) were used to examine differences in mass losses and litter quality (TC, TN, TC:TN, and TP; dependent variables) of the individual litter types within these peatlands over time (after 0, 20, 50, 250, 365, 465, and 730 days of decomposition; independent variables). This test was used due to the small sample size of decomposition bags per sample period per litter type (n = 4). Transformation of data did not remove the heterogeneity of variance or normalize the data. Tukey-type *post hoc* tests were performed to determine where significant differences were present within each of the data sets following the indication of significance in the Kruskal-Wallis analyses.

Pearson's correlation coefficients indicated if any of the environmental variables correlated to each other. Pearson correlation coefficients were also computed between mass losses of the individual litter types and litter quality (TC, TN, TC:TN, TP), environmental (surface water chemistry), and physical (peat and surface water temperature, depth of the acrotelm, water levels) variables in the bog and fen. Mean surface water chemistry, litter quality, and physical data at each sampling time were correlated with mass losses of the individual litters during each sampling period, *i.e.* means of these data from 0 to 20 days, 0 to 50 days, 0 to 8 months, etc... to reflect the mean conditions that the litters were exposed to during the varying incubation periods. Autocorrelations were performed on individual environmental variables to determine if successive data points within each site were related to another over time. Bonferroni tests ($p = 0.05$) provided probability values for all correlations. Two-tailed, paired t-tests were used to compare individual environmental variables between the bog and fen ($n = 21$ per variable).

Simple regressions were performed to develop statistical models for the masses remaining (dependent variable) of the litter types over the incubation periods in the field (independent variable). One day was added to each sample date to include the initial mass of each sample (day 1). Sample sizes were $n = 4$ for each of six sampling times ($n = 6$) for the five litter types over the two-year decomposition period. All statistical analyses were performed on SYSTAT (SYSTAT Inc. 1992).

RESULTS

Mass losses of decomposing belowground and aboveground plant tissues

Two-year mass losses of *Carex aquatilis* rhizomes (75%) were significantly higher ($p < 0.05$) than those of *Salix planifolia* leaves and *C. aquatilis* leaves, which were similar to each other (48 and 54%, respectively) ($p > 0.05$) (Figure 2-1). *Sphagnum fuscum* and *S. planifolia* root mass losses were similar to each other (21 and 29%, respectively) ($p > 0.05$), but they were significantly lower than those of the other three litter types over the same period ($p < 0.05$). Arith/log decomposition models (arithmetic/logarithmic, $y = \log(x) + b$) provided the best fit to the mass losses of the five litter types (Figure 2-1).

Nutrient tissue concentrations of decomposing plant tissues

TN tissue concentrations increased significantly in *Salix planifolia* roots and leaves ($p < 0.05$), but they did not change significantly in *Carex aquatilis* rhizomes and leaves and

Sphagnum fuscum over the two-year decomposition period ($p > 0.05$) (Figure 2-2). TP tissue concentrations showed a variable pattern, decreasing during the initial stages of decomposition before increasing in all litter types during the later stages of decomposition (Figure 2-2). Generally, *S. fuscum* and *C. aquatilis* rhizomes had the lowest tissue concentrations of TN and TP throughout the entire decomposition period (Figure 2-2). TC tissue concentrations did not change significantly throughout the two-year decomposition process for any of the litter types ($p > 0.05$). TC:TN quotients did not show any clear patterns, decreasing significantly only in *S. planifolia* leaves ($p < 0.05$), while remaining similar or fluctuating in the remaining four litter types over the two-year decomposition period ($p > 0.05$) (Figure 2-2).

TC tissue concentrations correlated with mass losses of both belowground litters over the first two years of decomposition (Table 2-1). TN tissue concentrations correlated with mass losses of *Salix planifolia* leaves and roots, while TP tissue concentrations were significantly correlated with mass losses of both leaf litters (Table 2-1). None of the litter quality variables significantly correlated with *Sphagnum fuscum* mass losses over the first two years of decay (Table 2-1).

Nearly two thirds of all the short-term accumulated sedge peat and carbon originated from aboveground *Carex aquatilis* tissues (Table 2-2). Conversely, both *Salix planifolia* litters had similar amounts of mass and carbon remaining after one and two years of decomposition (Table 2-2), despite significantly different mass losses over that period (Figure 2-1). In the bog, 150 g m^{-2} of the original *Sphagnum fuscum* litter remained after two years. With a carbon content of 470 mg g^{-1}, this amounts to an accumulation of 71 g C m^{-2} within this period (Table 2-2). These peat and carbon accumulation potentials are similar to those of the *Carex aquatilis* leaf litter in the riverine sedge fen (Table 2-2).

Relationship between environmental variables and mass losses of the decomposing plant tissues

The two peatlands differed significantly in most of their surface water chemistry from 1997 to 1999. Only nitrogen- and temperature-related variables did not differ significantly between these two peatlands ($p > 0.05$) (Table 2-3). Phosphorus-related surface water chemistry variables correlated significantly with mass losses of *Sphagnum fuscum* in the bog and *Carex aquatilis* leaves and rhizomes in the fen (Table 2-4). Surface water concentrations of Ca^{2+} correlated significantly with mass losses of all four fen litter types (Table 2-4). In addition, NH_4^+ concentrations correlated significantly with mass losses of both leaf litters for *C. aquatilis* and *Salix planifolia* leaves (Table 2-4).

DISCUSSION

Decomposition of *Salix planifolia* roots and leaves, *Carex aquatilis* rhizomes and leaves, and *Sphagnum fuscum*

Two-year mass losses of *Carex aquatilis* rhizomes were significantly higher than those of the other four litter types (Figure 2-1). The leaf litters lost similar amounts of mass over the two-year decomposition period but they significantly exceeded those of *Salix planifolia* roots and *Sphagnum fuscum* (Figure 2-1).

The arith/log model best described mass losses of the five litters types in this study (Figure 2-1). This model was first introduced by Thormann and Bayley (1997a) and differs from the widely used log/arith (logarithmic/arithmetic, log(y) = x + b) model developed by Jenny et al. (1949) and later adopted by Olson (1963) and Wieder and Lang (1982) to describe mass losses of plant litters under natural conditions in many ecosystems. Thormann and Bayley (1997a) suggested that the arith/log model might have provided a better fit to their data than the log/arith model because of the early sampling time of the vegetation used in their decomposition study (June). However, in this study, I collected the litters in early September and *Carex* and *Salix* leaves already had begun to senesce. Again, the arith/log model proved to describe mass losses of these litters better than the previously used log/arith model over the two-year decomposition period.

Decomposition of belowground plant litters

Two-year mass losses of *Carex aquatilis* rhizomes and *Salix planifolia* roots were 75 and 29%, respectively, and differed significantly (Figure 2-1). My first year mass loss of *C. aquatilis* rhizomes was 60% (Figure 2-1). This value is substantially higher than rhizome/root mass losses reported by Hackney and de la Cruz (1980), Buth (1987), Hemminga et al. (1988), Benner et al. (1991), and Pozo and Colino (1992) for salt marsh plant species, by Hartmann (1999) for freshwater wetland plant species, and by Heal et al. (1978) for bog plant species (Table 2-5).

It is interesting that few studies have examined decomposition rates of belowground tissues of wetland plant species, since a number of studies have suggested that the belowground biomass of some peatland plant species may significantly exceed that of the aboveground biomass (Bernard and Fiala 1986, Wallén 1986, Backéus 1990, Saarinen 1996). Rhizomes form most of the belowground biomass of *Carex* species in arctic ecosystems (59%) (Carlsson et al. 1990), while fine roots are more prevalent at more temperate latitudes (78-90%) (Bernard 1973, Saarinen 1996), a reflection of deeper soil horizons and greater water and nutrient availability at more southern latitudes. Fine roots appear to be the principal nutrient-absorptive organs and extend to great depths, often to the mineral soil horizon underlying the organic soil horizon (Saarinen 1996). However, Brooker et al. (1999) determined that rhizomes of *Carex bigelowii* Torr. *ex* Schwein. aid in the acquisition of N from the soil solution and fine roots are not the only nutrient-absorptive organs.

While rhizomes vary in longevity, depending on the species of *Carex* (Bernard and Fiala 1986), the fine roots of sedges and woody plant species are short-lived and have rapid turn-over rates, thereby constituting a major component of carbon and nutrient cycles in many ecosystems (Saarinen 1996). Previous studies in forest ecosystems indicate that fine roots of woody plant species account for up to 75% of the total net primary production (Persson 1978, Fogel 1983, Nadelhoffer and Raich 1992, Burke and Raynal 1994) and lose between 12 and 25% of their mass within the first year of decomposition (Fogel and Hunt 1979, Berg 1981, McClaugherty et al. 1982). Those mass losses are similar to the mass losses I observed for *Salix planifolia* roots after two years (29%; Figure 2-1). In contrast, mass losses of roots of woody plant species in the Great Dismal Swamp (Tupacz and Day 1990) generally exceeded those of *S. planifolia* in my study (Table 2-5), which can be attributed to differences in the plant litter quality and environmental conditions for those studies. These data further confirm the importance of examining belowground plant litters in the nutrient budget of peatlands.

Decomposition of aboveground plant litters

Carex aquatilis leaves lost 38 and 54% of their mass after one and two years, respectively (Figure 2-1). First-year mass losses in my study are similar to *Carex* leaf litter mass losses reported previously by Verhoeven and Arts (1992) (27-45%, floating fen, The Netherlands), Szumigalski and Bayley (1996a) (31-45%, boreal rich fens, Alberta), Thormann and Bayley (1997a) (50-59%, boreal rich fens, Alberta), and Arp et al. (1999) (58%, sub-alpine rich fens, Colorado), but are higher than those reported by Bartsch and Moore (1985) (6-27%, sub-arctic fen, Québec).

Mass losses of *Salix planifolia* leaves were 43% after one and 48% after two years and were similar to those of *Carex aquatilis* leaves (Figure 2-1). These results contradict those of Thormann and Bayley (1997a), who determined mass losses of *Salix pedicellaris* Pursh leaves to be significantly lower than those of *Carex lasiocarpa* leaves in a rich fen 1 km west of this sedge fen. These differences can be explained in part by the use of different species of *Carex* and *Salix* and significantly lower surface water phosphorus concentrations in their floating sedge fen compared to this riverine sedge fen (Table 2-3). Although decomposition rates of *Salix* litter are rarely measured in peatlands, my data are within the range reported by Heal and French (1974) (33%, bog, Norway) and Thormann and Bayley (1997a) (42%, rich fen, Alberta). However, *Salix* spp. mass losses in a sub-arctic fen were substantially lower (Bartsch and Moore 1985) (17%, Québec).

Sphagnum fuscum mass losses

Sphagnum fuscum lost 16% and 21% of its mass after one and two years, respectively, with the majority of these mass losses occurring within the first 20 days of decomposition (16%) (Figure 2-1). After 20 days, mass losses are nearly linear up to two years and only an additional 5% of mass was lost (Figure 2-1). These mass loss values are similar to those reported in previous studies and are comparable to those of *Salix planifolia* roots (Figure 2-1). Szumigalski and Bayley (1996a) reported first- and second-year mass losses of 14 and 15%, respectively, in a bog approximately 55 km north of my bog. *Sphagnum* mass losses were just over 10% after 14 months in a bog in northwestern Ontario, Canada (Rochefort et al. 1990) and after 10 months in a bog in Sweden (Johnson and Damman 1991).

The difference in mass losses between this and other studies can, in part, be explained by species, surface water chemistry, environmental, and methodological differences inherent to these studies. For example, the use of different plant species and tissues (leaves, petioles, stems, and/or mixtures thereof) will result in different mass losses due to inherently different tissue nutrient concentrations. Moreover, decomposition studies at higher latitudes indicate lower mass losses for similar litter types (Bartsch and Moore 1985). These may result from lower temperatures and soil and water nutrient concentrations at higher latitudes, factors that have been implicated previously in lower decomposition rates (Clymo 1965, Bridgham and Richardson 1992, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a). Furthermore, the degree of senescence (Ohlson 1987), drying temperature (Clymo 1965), and placement of the plant litter within the peat horizon (Santelmann 1992) affect decomposition rates and result in differences among studies.

The role of litter quality on mass losses

Total carbon tissue concentrations

Initial TC tissue concentrations were similar for all five litter types, ranging from 430 (*Carex aquatilis* rhizomes) to 470 mg g^{-1} (*Salix planifolia* leaves) and did not change significantly during the two-year decomposition period (Figure 2-2). These values are similar to those reported previously from southern boreal and sub-alpine bog and fen vegetation (Szumigalski and Bayley 1996a, Thormann and Bayley 1997a, Hartmann 1999, Arp et al. 1999).

TC tissue concentrations correlated significantly with mass losses of *Carex aquatilis* rhizomes and *Salix planifolia* roots (Table 2-1). Roots and rhizomes are the principal nutrient storage organs of many plant species during late fall, winter, and early spring and many woody and herbaceous plant species translocate photosynthates and nutrients from aboveground tissues into roots and rhizomes prior to their senescence and death (Berendse and Jonasson 1992). This leaves more recalcitrant molecules in the leaves and increases the concentrations of more labile and smaller molecules in the belowground tissues. This may explain the significant correlation between mass losses and TC tissue concentrations of *S. planifolia* roots and *C. aquatilis* rhizomes (Table 2-1).

Short-term peat and carbon accumulation potentials of these five litters were calculated using previously reported NPP values for species of *Carex* and *Salix* (Szumigalski and Bayley 1996b, Thormann and Bayley 1997b) and the estimated proportion of below- to aboveground plant production in western continental fens and bogs (1:1; Campbell et al. 2000). Using these data, almost two thirds of the total accumulated sedge peat (61%) and carbon (65%) in the riverine sedge fen originated from *Carex aquatilis* leaves, with the remainder originating from *C. aquatilis* rhizomes (Table 2-2) after the first two years of decomposition. This disparity resulted from the significantly higher rate of decomposition of the rhizomes (75%) compared to the leaves (54%) over the two-year decomposition period (Figure 2-1) and the use of a very conservative equal partitioning of above- and belowground NPP (Campbell et al. 2000). The ratio of the above- to belowground plant tissue contribution to the peat and carbon accumulation potential would be more similar if a less conservative estimate of the contribution of the belowground plant tissues to the total plant production is used in the calculations. Most of the belowground plant tissues (rhizomes and roots, the latter were not measured as part of this study) are located in the catotelm and receive oxygen through aerenchyma tissues (Fagersted 1992, Jackson and Armstrong 1999). Therefore, the combination of high belowground NPP and significantly lower rates of decomposition in the catotelm (Damman 1996) result in a significant contribution of belowground plant tissues to the development of peatlands characterized by a significant presence of rhizomatous plant species, such as species of *Carex*.

Despite significantly different rates of decomposition (Figure 2-1), *Salix planifolia* leaves and roots contribute similar amounts of peat and carbon to the fen (Table 2-2). However, due to their low NPP, their contribution to the accumulation of peat and carbon in the riverine sedge fen is negligible compared to the contribution of the *Carex* litters (Table 2-2). The peat and carbon accumulation potentials of *Sphagnum fuscum* over the first two years of decomposition in the bog are similar to those reported by Thormann et al. (1999a). This suggests that rates of peat and carbon accumulation are similar among bogs in southern boreal Alberta.

Total nitrogen tissue concentrations

Initial TN concentrations ranged from 6.8 mg g^{-1} in *Sphagnum fuscum* to 20 mg g^{-1} in *Carex aquatilis* leaves and they increased significantly over the two-year decomposition period in the *Salix planifolia* litters, but not in the sedge and bryophyte litters (Figure 2-2). The TN tissue concentrations of the bryophyte litter were always lower than those of the fen vascular plant litters (Figure 2-2). My TN values are similar to those of Szumigalski and Bayley (1996a), Bartsch and Moore (1985), Ohlson (1987), Thormann and Bayley (1997a), and Arp et al. (1999). Non-significant changes in tissue TN concentrations have been reported previously (Szumigalski and Bayley 1996a) and may indicate similar rates of losses of N due to leaching and microbial assimilation during the process of decomposition. Only the mass losses of the *Salix* litters were correlated significantly with TN tissue concentrations (Table 2-1). Both of these litters had similar initial TN tissue concentrations; however, they diverged during the decomposition process, with the leaf litter having significantly higher tissue concentrations of TN after two years (Figure 2-2). This partially contributed to significantly higher mass losses for *S. planifolia* leaves compared to roots over the two-year decomposition period (29 vs. 48%, respectively) (Figure 2-1).

TC:TN quotients

The initial TC:TN quotient of the litter is important in the decomposition process, because microbial populations (fungi and bacteria) accumulate nutrients, such as N, P, or K, during the early stages of decomposition (Verhoeven et al. 1990, Taylor et al. 1991) and low concentrations of these nutrients in the litter may lead to lower decomposition rates. In this study, TC:TN quotients decreased significantly only in *Salix planifolia* leaves, while remaining similar in the other four litter types (Figure 2-2). My TC:TN quotients are similar to those previously reported from bog and fen vegetation in North America (Szumigalski and Bayley 1996a, Thormann and Bayley 1997a, Arp et al. 1999). Initial TC:TN quotients ranged from 22 in *Carex aquatilis* leaves to 68 in *Sphagnum fuscum* and decreased slightly, but not significantly, over the two-year decomposition period (Figure 2-2). These decreases are the result of increasing TN and constant TC tissue concentrations (Figure 2-2). Although TC:TN quotients were negatively correlated with mass losses of all five litter types, the correlation was significant only for *S. planifolia* leaves (Table 2-1).

Net immobilization of N occurs at TC:TN quotients above approximately 30 (Parnas 1974), resulting in decreases of the TC:TN quotient over time. Conversely, net mineralization occurs at lower TC:TN quotients due to the equal utilization of N and C by microbial populations, resulting in insignificant changes in the TC:TN quotient (Verhoeven et al. 1990). The initial TC:TN quotients of four of the five litter types were above 30 (*Sphagnum fuscum*, *Salix planifolia* leaves and roots, *Carex aquatilis* rhizomes) and they all decreased during the decomposition process, albeit significantly only in *S. planifolia* leaves (Figure 2-2). This suggests that net immobilization, rather than mineralization, occurred. Conversely, the initial TC:TN quotient of *C. aquatilis* leaves was below 30 and it changed very little between sampling periods (Figure 2-2).

Mass losses over the first two years of decomposition could not be predicted based on the TC:TN quotients. Neither the initial TN tissue concentrations, nor the initial TC:TN quotient of the litter is indicative of decomposition rates in this study, contradicting previous results by Taylor et al. (1991), Verhoeven et al. (1992), Szumigalski and Bayley (1996a), and Thormann and Bayley (1997a), who determined that litters with lower initial TC:TN quotients, and hence higher initial TN tissue concentrations, have higher decomposition rates.

Total phosphorus tissue concentrations

Initial TP tissue concentrations ranged from 0.5 (*Sphagnum fuscum*) to 2.1 mg g^{-1} (*Carex aquatilis* rhizomes) (Figure 2-2). During the two-year decomposition period, TP tissue concentrations showed a variable pattern, decreasing substantially during the early stages of decomposition before increasing during the later stages of decomposition (Figure 2-2). Decreases in TP tissue concentrations of aboveground litter during the process of decomposition have been reported previously by Puriveth (1980), Verhoeven and Arts (1992), and Davis and van der Valk (1978). Decreases in P tissue concentrations in litter has been attributed to leaching during the early stages of decomposition. Subsequent increases in TP tissue concentrations have been attributed to assimilation by microbial populations from the surrounding water or soil solution and absorption by the decomposing plant materials (Puriveth 1980) during the later stages of decomposition.

TP concentrations were significantly correlated with the decay of both leaf litters (Table 2-1), indicating that higher concentrations of TP in *Carex aquatilis* and *Salix planifolia* leaves resulted in increased mass losses. This trend does not apply to *C. aquatilis* rhizomes, which lost significantly more mass than the other four litter types (Figure 2-1) and showed a negative correlation (not significant) between mass losses and TP tissue concentrations (Table 2-1). However, *C. aquatilis* rhizomes had significantly higher initial tissue concentrations of TP (2.1 mg g^{-1}) (Figure 2-2), which may partially account for the large mass losses observed in this study.

Mass losses of *Salix planifolia* roots in the riverine sedge fen were similar to those of *Sphagnum fuscum* in the bog (29 and 21%, respectively) after two years (Figure 2-1). These litter types differ significantly in TN and TP tissue concentrations, with the *S. planifolia* roots having significantly higher tissue concentrations of both tissue nutrients (Figure 2-2). Furthermore, surface water nutrient concentrations were significantly higher in the fen than the bog (Table 2-3) and should have contributed to higher mass losses of the root litter than the bryophyte litter. Despite the greater availability of nutrients to microbial communities in the fen, it is possible that the root litter had higher concentrations of recalcitrant, structural polymers, such as lignin and cellulose, than the bryophyte litter, thereby decreasing decomposition rates. Similarly, mass losses of *Carex aquatilis* rhizomes significantly exceeded those of *C. aquatilis* leaves (74 *vs*. 54%, respectively) (Figure 2-1), despite significantly lower tissue concentrations of TN and TP throughout the first two years of decomposition (Figure 2-2). Hartmann (1999) determined that initial TN tissue concentrations of belowground tissues did not correlate with first year mass losses of her fen vegetation, indicating an inverse relationship between initial TN tissue concentrations and mass losses. Although neither she, nor I, measured cellulose and lignin tissue concentrations of our litters, Coulson and Butterfield (1978) suggested that the amount of cellulose associated with lignin (lignocellulose) affects mass losses of plant litters. Plant litters with high concentrations of lignocellulose are very resistant to decomposition (Benner et al. 1984).

Fungi

Physical characteristics of the litter types may significantly affect mass losses and may be more important than either environmental or litter quality variables. Litter that provides a large surface area for microbial (fungi and bacteria) attack may decompose faster than litter with a comparatively smaller surface area, despite a lower nutrient availability to microbial populations in the former litter type (Seliskar et al. 1977). Although *Salix planifolia* fine roots and *Carex aquatilis* rhizomes may have similarly large surface areas for microbial attack, the root litter may have larger concentrations of decomposition-resistant materials, such as lignin and other phenolic compounds. The presence of ectomycorrhizal fungal mycelium may increase cell wall lignification (Campbell and Ellis 1992) and phenolic (Horan et al. 1988) compound deposition by the host plant near the contact zone with the fungus as a defense mechanism. This may result in lower mass losses compared to non-mycorrhizal or non-ectomycorrhizal plant tissues, such as *C. aquatilis* rhizomes (Thormann et al. 1999b, Chapter 6) or aboveground plant tissues. Roots of *S. planifolia* were ectomycorrhizal in the riverine sedge fen (Thormann et al. 1999b, Chapter 6). These fungi form a Hartig net and mantle in and around the roots of the host plant. Furthermore, the principal structural cell wall component of fungi is chitin and it is broken down poorly if at all through the saprophytic activities of other fungi (Carlile and Watkinson 1994). Thus, higher *C. aquatilis* rhizome mass losses could be the result of increased surface area for microbial attack due to aerenchyma tissue (oxygen-conducting tissues) (Fagersted 1992, Jackson and Armstrong 1999), significantly higher initial TP tissue concentrations (Table 2-1), and the absence of ectomycorrhizal fungal tissues (Thormann et al. 1999b, Chapter 6).

The role of surface water chemistry variables on mass losses

Alkalinity-related surface water variables were negatively correlated with mass losses of the above- and belowground litter types in the riverine sedge fen (Table 2-4). Similar negative correlations between acidity-alkalinity gradient variables and mass losses in southern boreal poor and rich fens were previously reported by Szumigalski and Bayley (1996a), who suggested that decomposition of their litter was inhibited by increased alkalinity, *i.e.* higher pH. In contrast, Tóth and Zlinszky (1989) and Verhoeven et al. (1990) found that decomposition of plant litter was inhibited at low pH. However, Farrish and Grigal (1988) and Bridgham and Richardson (1992) suggested that only anaerobic decay of plant litter is retarded at low pH and that aerobic decay may be unaffected or slightly enhanced by a decreasing pH. My data support their hypothesis. Similarly, conductivity, alkalinity, and HCO_3^- surface water concentrations (Table 2-4) may have retarded mass losses of both *Carex aquatilis* litters and *Salix planifolia* leaves. Also, most fungi are acidophiles and fungi constitute the dominant decomposer community in low pH ecosystems compared to bacteria (Latter et al. 1967). Therefore, a lower pH likely enhances their abilities to decompose plant litters.

TDP and NH_4^+ surface water concentrations correlated positively with mass losses of both *Carex aquatilis* litter types and *Salix planifolia* leaves (Table 2-4). This suggests that their decomposition may be enhanced by a higher nutrient-availability to decomposer microbial populations, thereby supporting results by Coulson and Butterfield (1978), Slapokas and Granhall (1991), and Szumigalski and Bayley (1996a). Conversely, other studies suggest that wetlands richer in nutrients do not have higher decomposition rates (Bayley et al. 1985, Rochefort et al. 1990, Bridgham and Richardson 1992). Thormann and Bayley (1997a) determined that increased TDP surface water concentrations were negatively correlated with mass losses of *C. aquatilis* leaves in the same fen. In addition, mass losses of *Sphagnum fuscum* in the bog were negatively correlated with TP surface water concentrations (Table 2-4). These conflicting data suggest that other variables may be more important in the decomposition of plant litters in peatlands, such as water levels (Thormann et al. 1999a), litter quality and morphology, or the composition of microbial communities.

CONCLUSIONS

This is the first study that examined decomposition rates of belowground litter of the dominant sedge and shrub species and compared them to the aboveground plant litters in North American peatlands. Mass losses of *Carex aquatilis* rhizomes (75%) significantly exceeded those of *C. aquatilis* leaves (54%), *Salix planifolia* leaves (48%), and *S. planifolia* roots (29%) in a rich fen and *Sphagnum fuscum* (21%) in a bog after two years. Mass losses of the aboveground plant litters of the fen vegetation and the bog bryophyte were similar to those reported in previous studies in North America and Europe. Mass loss differences could only partially be explained by differences in litter quality or surface water chemistry and other variables, such as lignin, cellulose, chitin, and/or other elemental nutrient concentrations, as well as litter morphology or different microbial populations, may influence decomposition rates.

Due to the large contribution of belowground tissues of many wetland plant species to the total plant production, these tissues constitute a major component of carbon and nutrient cycles in wetlands. Decomposition rates of *Carex aquatilis* rhizomes are high in the acrotelm. These rates, however, may decrease significantly in the catotelm under anoxic conditions and, along with fine roots, rhizomes constitute a significant contribution to peat and carbon accumulation in sedge-dominated wetlands. My data indicate that nearly one third of all the sedge peat and carbon originates from rhizomatous plant tissues in this fen. I did not examine decomposition rates of *C. aquatilis* roots; however, they too constitute a significant portion of the total belowground production and would have increased the importance of belowground plant tissues relative to aboveground plant tissues in the development of peatlands in boreal Canada.

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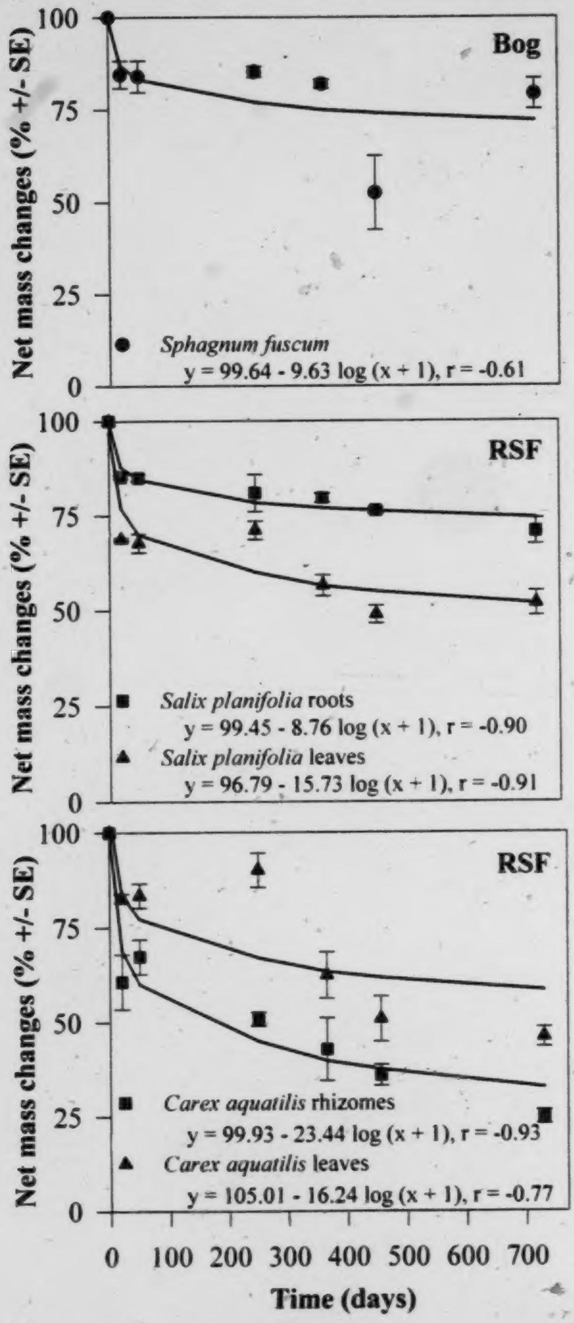

Figure 2-1. Net mass changes of the dominant indigenous plant species over 20 and 50 days and eight, 12, 20, and 24 months from September 1997 to September 1999 in two peatlands in southern boreal Alberta, Canada. RSF, riverine sedge fen.

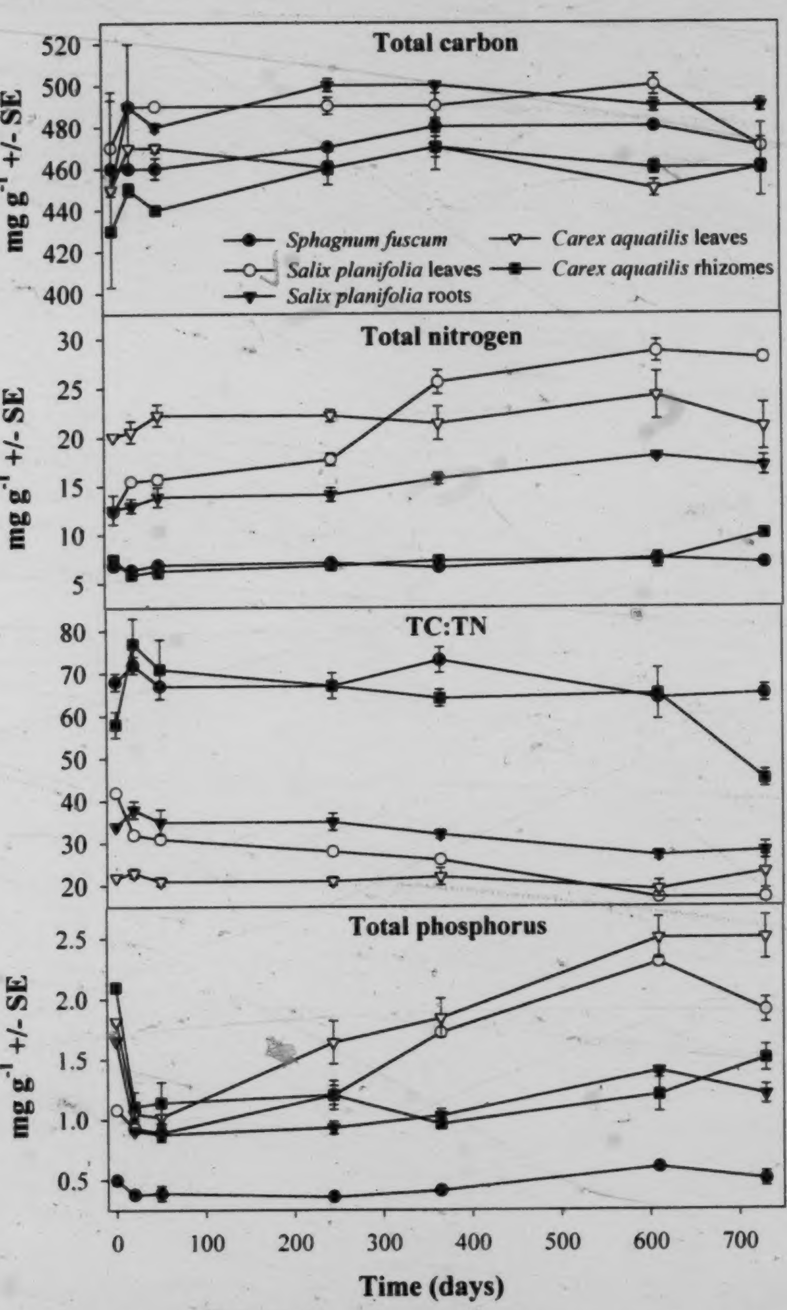

Figure 2-2. Mean litter quality (mg g^{-1} +/- SE) of the plant litters in the bog (*Sphagnum fuscum*) and riverine sedge fen (*Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots) from September 1997 to September 1999 in southern boreal Alberta, Canada. Note the different scales on the y-axes.

Table 2-1. Pearson's correlation coefficients of 2-year mass losses of the dominant plant species in the bog and riverine sedge fen (RSF) and litter quality variables.

Sites	Litter types	TC	TN	TC:TN	TP
Bog	*Sphagnum fuscum* plants	0.32	0.46	-0.42	0.55
RSF	*Salix planifolia* leaves	0.50	0.87 ***	-0.91 ***	0.68 **
	Salix planifolia roots	0.58 *	0.73 **	-0.57	-0.20
	Carex aquatilis leaves	-0.04	0.19	-0.08	0.70 *
	Carex aquatilis rhizomes	0.81 ***	0.39	-0.20	-0.47

Note: TC = total carbon, TN = total nitrogen, TP = total phosphorus, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Table 2-2. Litter masses and peat and carbon accumulation values from the five litter types in the bog and riverine sedge fen (RSF) prior to and after 1 and 2 years of decomposition.

		Initial			Year one			Year two		
		Total NPP	Carbon		Masses remaining	Carbon		Masses remaining	Carbon	
Sites	Litter types	(g m^{-2} yr^{-1})	(mg g^{-1})	(g m^{-2})	(g m^{-2})	(mg g^{-1})	(g m^{-2})	(g m^{-2})	(mg g^{-1})	(g m^{-2})
Bog	*Sphagnum fuscum* plants	190 *	460	87	160	480	77	150	470	71
RSF	*Salix planifolia* leaves	46 *	470	22	26	490	13	24	470	11
	Salix planifolia roots	46 **	450	21	36	500	18	33	490	16
	Carex aquatilis leaves	409	450	184	254	470	119	188	460	86
	Carex aquatilis [illegible]	409 **	430	176	172	470	81	102	460	47

Note: * Mean estimates from bog and moderate-rich and rich fen NPP data in Thormann and Bayley (1997b), ** estimate of the proportion of belowground NPP (50%) to the total NPP in boreal peatlands (Campbell et al. 2000). NPP is net primary production.

Table 2-3. Mean environmental variables (surface water chemical and physical variables, means ± SE) of the bog and the riverine sedge fen in Alberta, Canada, from 1997 to 1999 .

Variables	Perryvale Bog	Riverine sedge fen	p
pH	3.8 (0.03)	6.9 (0.10)	***
Conductivity † ($\mu S\ cm^{-1}$)	66 (7)	196 (19)	***
Alkalinity ($mg\ L^{-1}\ CaCO_3$)	0 (-)	105 (10)	***
HCO_3^- ($mg\ L^{-1}$)	0 (-)	128 (12)	***
NO_3^- ($\mu g\ L^{-1}$)	8 (1)	9 (2)	n.s.
NH_4^+ ($\mu g\ L^{-1}$)	10 (4)	13 (4)	n.s.
Total dissolved nitrogen ($\mu g\ L^{-1}$)	1,121 (62)	1,040 (68)	n.s.
Soluble reactive phosphorus ($\mu g\ L^{-1}$)	9 (4)	96 (36)	*
Total phosphorus ($\mu g\ L^{-1}$)	140 (41)	970 (274)	**
Total dissolved phosphorus ($\mu g\ L^{-1}$)	36 (13)	125 (37)	*
Dissolved organic carbon ($mg\ L^{-1}$)	58 (2)	28 (2)	**
K^+ ($mg\ L^{-1}$)	0.4 (0.1)	1.5 (0.5)	*
Ca^{2+} ($mg\ L^{-1}$)	3 (0.3)	28 (3)	**
Peat temperature (°C)	7 (1)	8 (1)	n.s.
Water temperature (°C)	5 (1)	9 (1)	n.s.
Water level ‡ (cm)	-37 (6)	1 (5)	***
Depth of acrotelm ‡ (cm)	-47 (3)	-6 (3)	***

† Conductivity is adjusted for temperature and pH. ‡ Water levels and depths of the acrotelm are with respect to the moss/peat surface. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$, n.s. = not significant.

Table 2-4. Pearson's correlation coefficients of 2-year mass losses of the dominant plant species in the bog and riverine sedge fen (RSF) and surface water chemistry variables.

Sites	Litter types	Surface water chemistry variables	r
Bog	*Sphagnum fuscum* plants	Total phosphorus	-0.826 ***
RSF	*Salix planifolia* leaves	Calcium	-0.871 ***
		Conductivity (adjusted)	-0.717 *
		Ammonium	0.679 *
	Salix planifolia roots	Calcium	-0.851 ***
	Carex aquatilis leaves	Total dissolved phosphorus	0.851 ***
		Soluble reactive phosphorus	0.840 **
		Ammonium	0.838 **
		Calcium	-0.712 *
	Carex aquatilis rhizomes	Calcium	-0.846 ***
		Conductivity (adjusted)	-0.774 **
		Total dissolved phosphorus	0.735 *
		Alkalinity	-0.729 *
		Bicarbonate	-0.729 *

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Only significiant variables are shown.

Table 2-5. Mass losses of belowground plant tissues in wetland ecosystems after 1 year.

References	Locations	Plant species and litter types	Mass losses (%)
This study	Riverine sedge fen, AB, Canada	*Carex aquatilis* rhizomes	60
		Salix planifolia roots	20
Tupacz and Day (1990)	Great Dismal Swamp, VA/NC, U.S.A.	*Chamaecyparis thyoides* (L.) BSP. roots	26
		Quercus spp. roots	35
		Taxodium distichum (L.) Rich. roots	36
		Acer rubrum L. and *Nyssa* spp. roots	40
Wrubleski et al. (1997)	Freshwater marsh, MB, Canada *	*Scolochloa festucaceae* (Willd.) Link roots/rhizomes	60 - 67
		Phragmites australis (Cav.) Trin. *ex* Steud. roots/rhizomes	58 - 77
		Scirpus lacustris L. roots/rhizomes	38 - 58
		Typha glauca Godr. roots/rhizomes	48 - 54
Benner et al. (1991)	Salt marsh, GA, U.S.A.	*Spartina alterniflora* Loisel. roots/rhizomes	53
Hemminga et al. (1988)	Salt marsh, The Netherlands **	*Spartina anglica* Hubbard roots/rhizomes	37 - 55
Puriveth (1980)	Freshwater marsh, WI, U.S.A.	*Typha latifolia* L. roots/rhizomes	72
		Sparganium eurycarpum Engelm. *ex* Gray roots/rhizomes	58
		Scirpus fluviatllis (Torr.) Gary roots/rhizomes	40
Pozo and Colino (1992)	Salt marsh, Spain	*Spartina maritima* (Curt.) Fernald roots/rhizomes	42

Hartmann (1999)	Rewetted fen, Germany	*Carex riparia* Curtis roots	47
		Carex paniculata L. roots	31
		P. australis roots	15
Buth (1987)	Salt marsh, The Netherlands ***	*Puccinellia maritima* (Huds.) Parl. roots	32
		Halimione portulacoides (L.) Aellen roots	27
		S. anglica roots	18
Hackney and de la Cruz (1980)	Tidal marsh, MS, U.S.A.	*Juncus roemerianus* Scheele roots	27
		Spartina cynosuroides (L.) Roth roots/rhizomes	21
		J. roemerianus rhizomes	16
Heal et al. (1978)	Bog, U.K.	*Eriophorum vaginatum* L. roots	12
		Calluna vulgaris (L.) Hull belowground stems	7
		C. vulgaris roots	5

Note: * Different flooding regimes; ** Three different aquatic ecosystems, mass losses at 3 cm depth; *** 30 weeks decomposition period, mass losses at 10 cm depth.

CHAPTER 3. FILAMENTOUS MICROFUNGI FROM THE LIVING AND DECOMPOSING DOMINANT VEGETATION OF TWO PEATLANDS IN SOUTHERN BOREAL ALBERTA, CANADA

INTRODUCTION

Peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and 16% of Alberta's land base (Vitt et al. 1996). Of Alberta's landscape, 4.9% are bogs and the remaining 11.4% are fens (Vitt et al. 1996). Bogs are ombrotrophic ecosystems that receive water and nutrients solely from precipitation. Bogs are dominated by species of *Sphagnum*, *Picea mariana* (Mill.) BSP., and members of the Ericaceae, including species of *Rhododendron*, *Andromeda*, and *Vaccinium*. Conversely, fens are minerotrophic ecosystems that receive water and nutrients from precipitation and ground and/or surface water flow. Fens can be subdivided into poor and rich fens. Poor fens are characterized by low mineral ion concentrations in the surface water and few moss indicator species, most of which are species of *Sphagnum* (Vitt 1994). In contrast, rich fens are characterized by high mineral concentrations in the surface water and an increasing number of moss indicator species, such as species of *Drepanocladus*, *Scorpidium*, and *Aulacomnium* ("brown" mosses) (Vitt 1994). Additionally, shrubs, such as species of *Salix* and *Betula*, and herbaceous plants, such as species of *Carex*, are found in both poor and rich fens.

Peatlands in western continental Canada have been accumulating peat (45-50% carbon (C) [Thormann et al. 1999a]) since the end of the last ice age, approximately 8,000 years ago (Halsey et al. 2000). It has been suggested that peat accumulation results from an imbalance between net primary production (NPP) and decomposition (Clymo 1965, Vitt 1990). Gorham (1990) estimated that northern peatlands store between 180 and 277 Gt C (1 Gt = 10^9 t), representing approximately 10-16% of the total terrestrial detrital carbon, making them some of the world's most important ecosystems (Gorham 1991).

The majority of peat that accumulates in western Canadian peatlands consists of moss- and sedge-remains (Kuhry and Vitt 1996) because mosses and sedges contribute significantly to the total NPP in western Canadian continental peatlands (Thormann and Bayley 1997). Because of the importance of peatlands to the global C cycle (Gorham 1991), it is important to understand the mycota involved in the decay of the dominant plant species in peatlands. Studies investigating microfungi of peatlands have been conducted in North America (Christensen and Backus 1961, Christensen and Whittingham 1965, Dooley and Dickinson 1971), Europe (Dal

Vesco 1974-75, Nilsson et al. 1992, Salo 1993), and Australia (McLennan and Ducker 1954, Thrower 1954). These studies have used a variety of isolation techniques, ranging from the dilution plate technique to directly plating peat onto fungal growth media. Species of *Penicillium*, *Mortierella*, *Mucor*, *Trichoderma*, and *Fusarium* have been encountered most frequently in these studies, although various ascomycetes, yeasts, and sterile taxa are listed also. All of the aforementioned studies investigated the mycota of peat, which is an assemblage of remains of bryophytes, roots, herbaceous and woody plants, invertebrates, and microbes, whereas the fungi associated with the dominant peat-forming plants have not been studied. Conversely, reports of fungi from aboveground plant tissues from a variety of vascular plant species are common and the available information has been summarized by Ellis and Ellis (1985), Ginns (1986), and Farr et al. (1989). Their host indices include chytridiomycetes, ascomycetes, basidiomycetes, and Fungi Imperfecti and encompass many wetland plant species. However, the mycota of belowground tissues of vascular plant species in any ecosystem, both living and decomposing, is also poorly understood.

The objectives of this study were to conduct a comprehensive investigation of the filamentous microfungi from the dominant plant species of two southern boreal peatlands in Alberta. These were *Sphagnum fuscum* (Schimp.) Klinggr. from a bog and *Carex aquatilis* Wahlenb. leaves and rhizomes and *Salix planifolia* Pursh leaves and roots from a fen.

METHODS

Study area and site descriptions

The riverine sedge fen and Perryvale bog lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). The area has mild summers and cold, snowy winters with a long-term mean annual temperature of 1.7 °C. The total mean annual precipitation is approximately 500 mm (Environment Canada 1982).

The riverine sedge fen is dominated by *Carex aquatilis*, *Carex lasiocarpa* Ehrh., *Salix planifolia*, and *Equisetum fluviatile* L. The bryophyte stratum is sparse and discontinuous and consists primarily of *Brachythecium mildeanum* (Schimp.) Schimp. *ex* Milde and *Tomenthypnum nitens* (Hedw.) Loeske. The Perryvale bog is dominated by *Sphagnum fuscum*, *Sphagnum angustifolium* (C. Jens *ex* Russ.) C. Jens, *Picea mariana*, and members of the Ericaceae, including *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Andromeda polifolia* L. Vegetation composition, surface water chemistry, and physical parameters of both sites are provided in more detail elsewhere (Thormann et al. 1999b, Thormann et al. 2001a).

Sampling of living and decomposing plant material

In the bog, the top 3 cm of approximately 20 individual living *Sphagnum fuscum* plants were collected in early May, July, and September 1997. In the fen, the top 10 cm of ten *Carex aquatilis* leaves, ten 10 cm segments of living *C. aquatilis* rhizomes, ten entire *Salix planifolia* leaves, and ten 10 cm terminal segments of *S. planifolia* roots were collected at the same time as the *S. fuscum* material.

A two-year decomposition study using nylon mesh bags (3 x 6 cm, 1 mm gauge) was initiated in early September 1997 (Thormann et al. 2001a, Chapter 2). Briefly, between five and eight individual fresh segments of each plant substrate were placed separately into each of 18 decomposition bags. A total of 90 decomposition bags were deployed in the peatlands and placed horizontally approximately 2-5 cm below the peat surface (*Sphagnum fuscum*, *Carex aquatilis* rhizomes, *Salix planifolia* roots) or on top of the peat surface (*S. planifolia*, *C. aquatilis* leaves) to mimic natural conditions of decomposition for these plant tissues. Sets of triplicate decomposition bags with the decomposing plant tissues were retrieved after 20 and 50 days in 1997, after eight and 12 months in May and September 1998, respectively, and after 20 and 24 months in May and September 1999, respectively.

Isolation and identification of filamentous microfungi

The living and decomposing plant material was cleaned by removing roots and other plant tissues using fine forceps and a dissecting microscope. The contents of all three decomposition bags retrieved at each decomposition period for each of the five plant tissues were combined prior to selecting sub-sets of these materials for further processing. Each of ten randomly selected, cleaned segments of each plant tissue was cut with a flame-sterilized scalpel into ten smaller segments (approximately 5 x 5 mm in size). These were surface-sterilized for five minutes in 10% hydrogen peroxide (H_2O_2) and washed with sterilized, distilled water (d-H_2O) prior to placing them on Potato Dextrose Agar (PDA, 39.0 g Difco potato dextrose agar, 1.0 L d-H_2O), PDA with rose bengal (0.03%), PDA with benomyl (0.0002%), and Mycobiotic agar® (MYC, containing cycloheximide, 35.6 g Difco mycobiotic agar, 1.0 L d-H_2O). All media were amended with oxytetracycline (0.01%) to suppress bacterial growth.

Plates were incubated at room temperature in the dark and fungi were sub-cultured onto Malt Extract Agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) as soon as they grew from the plant material. Plates were examined for emerging fungi daily for the first two weeks, weekly for the following six months, and monthly for the following two years of incubation. Plates with nematodes, mites, and other microinvertebrates were discarded to avoid cross-contamination. For identification purposes, slide cultures (Sigler 1993) on mixed cereal agar (Pablum®, H. J. Heinz Company of Canada Ltd., 100.0 g mixed cereal, 15.0 g Difco agar, 1.0 L d-H_2O) were prepared, mounted in polyvinyl alcohol, and examined on an Olympus BX50 compound microscope. Only fungi that produced distinctive diagnostic colony and morphological characters were enumerated. Yeasts and *mycelia sterilia* represented less than 20% of all isolates and along with chytridiomycetes were excluded from this study.

Isolates were scored as separate records if they originated from different plant segments on the same primary isolation plate or if they originated from plant segments from different primary isolation plates. Multiple isolates from the same plant segment were scored as a single record. Some fungi were selected to determine their abilities to degrade tannic acid, cellulose, starch, gelatin, and pectin (Hutchison 1990). The test for laccase followed Stalpers (1978). Representative living cultures and/or microscope slides have been deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH), the University of Alberta Cryptogamic Herbarium (ALTA), the Centraalbureau voor Schimmelcultures (CBS), and/or the Northern Forestry Centre (NoF).

Annotations

Morphological dimensions are given as "(minimum size)-mean size-(maximum size)" to provide an indication of the range of dimensions of individual morphological characters. Means are based on ≥10 measurements in all cases. This notation style differs from the traditional style, which usually provides only a range of dimensions of characteristic features of a particular fungus without indicating the mean dimensions. Each annotation provides the full name of each identified species and its authority, citation, and accession number. Only distinguishing or unusual colonial and/or morphological characteristics are provided in the annotations. These characters permit the separation of species within the genera isolated in this study. Information on the distribution, sources of isolates, and enzymatic capabilities of each fungal taxon is provided wherever such data could be found in the literature.

RESULTS AND DISCUSSION

Ninety-five fungal species were obtained during the survey of fungi from the dominant vegetation in a bog and fen in southern boreal Alberta (three ascomycetes, ten basidiomycetes, 12 zygomycetes, and 70 Fungi Imperfecti). The majority of these species represents new records from the five substrates (*Sphagnum fuscum* plants, *Salix planifolia* leaves and roots, and *Carex aquatilis* leaves and rhizomes). A total of 883 records of fungi was obtained and represented 33 genera. Fifteen species could not be identified but were described morphologically and physiologically. These included eight basidiomycetes and seven pycnidial taxa. The five genera with most species were *Mortierella* (11 species), *Penicillium* (eight species), *Trichoderma* (seven species), *Acremonium* (six species), and *Verticillium* (five species). These five genera accounted for 37 of the 95 species (39%) identified and/or described in this study and for 384 of 883 records (43%).

Although 95 different fungal species have been identified and/or described, there are undoubtedly many more fungi in these plant tissues. Primary isolation plates were observed frequently over the first six months of the study and all fungi growing out of the plant tissues were sub-cultured onto MEA; however, yeasts and those isolates that remained sterile even after two years and several attempts to induce sporulation (alternative growth media, refrigeration, "black light" exposure) were not included here. Furthermore, some fungi likely did not grow on the primary isolation medium. The number of records obtained from the primary isolation plates decreased significantly after six months and very few additional records were obtained. This may be due to a combination of having sub-cultured the majority of fungi in these litters at that time and/or faster growing fungi covering the primary isolation plates and slower growing fungi were missed subsequently.

Following are brief descriptions of the fungal taxa I isolated from living and decomposing *Sphagnum fuscum* from a bog, and *Salix planifolia* leaves and roots and *Carex aquatilis* leaves and rhizomes from a fen. Colony information, where provided, is based on descriptions from MEA unless stated otherwise. The following notations were used to indicate the number of records of a particular fungus from a particular substrate: D = from decomposing plant tissues and L = from living plant tissues, *e.g.* D – 2 indicates that a particular fungus was isolated twice from decomposing plant tissues of one of the five plant substrates.

Zygomycota

Mortierella alpina Peyronel, 1913, Dissertationes Padova, p. 27 (ALTA 10686).

From *S. fuscum* (D – 3). Sporangiophores simple, basally swollen; sporangiospores ellipsoidal to cylindrical, (3.5)-4.1-(5.0) µm x (1.5)-2.2-(2.5) µm; cosmopolitan; reported from soil, liver lesions of calf (see Domsch et al. 1980 for references); chitinolytic (Domsch 1960), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella elongata Linnem., 1941, Pflanzenforschung **23**: 43 (ALTA 10687).

From *C. aquatilis* rhizomes (L – 1) and leaves (D – 3), *S. planifolia* roots (D – 1), *S. fuscum* (L – 6, D – 12). Sporangiophores simple or basitonously branched; sporangiospores ellipsoidal to short-cylindrical, (6.0)-8.2-(10.0) µm x (3.0)-4.5-(6.0) µm; cosmopolitan; reported from soil, rhizosphere of plants (see Domsch et al. 1980 for references); weakly pectinolytic (Domsch and Gams 1969), chitinolytic (Jackson 1965), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella ericetorum Linnem., 1953, Zentralblatt der Bakteriologie II **107**: 225-230 (ALTA 10688).

From *S. planifolia* roots (L – 4). Sporangiophores simple; sporangiospores spherical to ovoid, warted, (5.5)-6.6-(7.5) µm; uncommon; reported from soil, root and leaf litter (Gams 1971).

Mortierella horticola Linnem., 1941, Pflanzenforschung **23**: 21 (ALTA 10691).

From *S. fuscum* (L – 1, D – 3). Sporangiophores simple or with one side-branch; stylospores spherical to globose, spinulose, (8)-11-(15) µm; cosmopolitan; reported from soil, roots of herbaceous plants (see Domsch et al. 1980 for references); chitinolytic (Jackson 1965).

Mortierella humilis Linnem., 1936, Flora **130**: 176-217 (ALTA 10692).

From *S. fuscum* (L – 1). Sporangiophores basitonously branched; stylospores spherical to globose, finely verrucose, (7)-11-(15) µm; cosmopolitan; reported from primarily acidic soils and compost (see Domsch et al. 1980 for references); chitinolytic (Gray and Baxby 1968), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella isabellina Oud. & Koning, 1971, Archives Neerlandaise des Sciences Exactes et Naturelles, Séries **7**: 266-298 (ALTA 10689).

From *C. aquatilis* rhizomes (D – 1) and leaves (L – 2), *S. planifolia* leaves (D – 1), *S. planifolia* roots (L – 2), *S. fuscum* (L – 1, D – 7). Sporangiophores simple or branched; sporangiospores globose to slightly angular, (2.2)-2.6-(3.1) µm; cosmopolitan; reported from soil and vegetation (see Domsch et al. 1980 for references).

Mortierella minutissima v. Tiegh., 1876, Annales des Sciences Naturelles. A. Botanique, Séries **4**: 385 (ALTA 10690).

From *S. planifolia* roots (D – 2), *C. aquatilis* rhizomes (D – 1) and leaves (L – 1, D – 1), *S. fuscum* (L – 7, D – 10). Sporangiophores simple or basitonously branched; sporangiospores globose, (3.5)-4.0-(5.0) µm; cosmopolitan; reported from soil and wood (see Domsch et al. 1980 for references); chitinolytic (Gray and Baxby 1968), ability to utilize other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella ramanniana var. *angulispora* (Möller) Linnem., 1971, Pflanzenforschung **23**: 19 (ALTA 10693).

From *S. fuscum* (L – 5, D – 9). Sporangiophores simple or branched; sporangiospores angular, smooth, (2.4)-3.0-(3.6) µm; cosmopolitan; reported from soil, decaying vegetation, dung, and animal tissues (see Domsch et al. 1980 for references); pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Mortierella ramanniana var. *ramanniana* (Naumov) Linnem., 1971, Pflanzenforschung **23**: 19 (ALTA 10694).

From *S. fuscum* (L – 2, D – 6). Sporangiophores simple or branched; sporangiospores oval to ellipsoid, smooth, (2.8)-3.3-(3.8) µm; cosmopolitan; reported from soil, decaying plants, dung, and animal tissues, primarily in temperate and subarctic regions (see Domsch et al. 1980 for references); pectinolytic, cellulolytic, utilizes starch (Flanagan and Scarborough 1974).

Mortierella renispora Dixon-Stewart, 1932, Transactions of the British Mycological Society **17**: 208-220 (ALTA 10695).

From *S. fuscum* (L – 2, D –4). Sporangiophores simple, with a broad basal foot; sporangiospores reniform, (4.0)-4.1-(4.5) µm x (1.5)-2.1-(2.5) µm; cosmopolitan; reported from soil (Dixon-Stewart 1932, Mehrotra and Mehrotra 1964).

Mortierella verticillata Linnem., 1941, Pflanzenforschung **23**: 22 (ALTA 10696).

From *S. fuscum* (L – 1, D – 1). Sporangiophores verticillately branched; stylospores spherical to globose, (7)-10-(13) µm; cosmopolitan; reported from soil and roots of plants (see Domsch et al. 1980 for references); chitinolytic (Gray and Baxby 1968).

Mucor hiemalis Wehmer, 1903, Annales Mycologici **1**: 39 (ALTA 10697).

From *C. aquatilis* rhizomes (D – 9) and leaves (L – 1, D – 5), *S. planifolia* roots (L – 3, D – 21) and leaves (L – 2, D – 11), *S. fuscum* (L – 10, D – 26). Sporangiophores simple or (slightly) sympodially branched, up to 1.8 cm long; sporangiospores ellipsoidal, (4.8)-5.6-(7.0) µm x (2.5)-3.1-(4.8) µm; cosmopolitan; reported from soil, vegetation, dung, and foods (see Domsch et al. 1980 for references); hemicellulolytic (Loub 1960), chitinolytic (Domsch 1960), pectinolytic (Domsch and Gams 1969), utilizes starch (Franz 1975), gelatinolytic.

Ascomycota

Kernia retardata Udagawa and Muroi, 1981, Transactions of the Mycological Society of Japan **22**: 18 (UAMH 9613).

From *S. fuscum* (L – 2). Ascomata black, spherical to pyriform, without neck, (140)-185-(250) µm; ascospores reddish-brown, reniform, single-celled, smooth, (5.0)-5.4-(6.0) µm x (3.0)-4.3-(5.0) µm; widespread; reported from decaying vegetation, foods, soils, dung (Lumley et al. 2000); cellulolytic, gelatinolytic, utilizes starch.

Anamorph a *Scopulariopsis*; conidia (4.0)-5.9-(7.0) µm x (2.0)-2.3-(2.5) µm (ALTA 10703).

Sordaria fimicola (Rob.) Ces. & de Not., 1948, Canadian Journal of Research, C, **26**: 486-497 (ALTA 10705, UAMH 9475).

From *S. fuscum* (L – 4). Ascospores broadly fusiform to ovoid and/or subglobose, germ pore, gelatinous sheath, single-celled, (20)-23-(26) µm x (10)-13-(15) µm; cosmopolitan; reported from a variety of substrates, principally the dung of herbivores and soil (see Domsch et al. 1980 for references); cellulolytic, utilizes starch.

Sporormiella intermedia (Auersw.) Ahmed & Cain, 1969, Bulletin. National Science Museum, Tokyo **12**: 311-430 (ALTA 10706).

From *S. fuscum* (L – 1). Ascospores dark brown to black at maturity, multiseptate (typically triseptate) with constrictions at septa, gelatinous sheath, oblique germ slits, (50)-58-(65) µm x (10)-12-(13) µm; widespread; reported from herbivore and carnivore dung (Ahmed and Cain 1972); utilizes starch.

Basidiomycota

Armillaria sinapina Bérubé & Dessur., 1988, Canadian Journal of Botany 66: 2030-2033 (UAMH 9792, NoF 2375 to 2380).

From *C. aquatilis* rhizomes (L – 1) and leaves (D – 2), *S. planifolia* leaves (D – 3). Colonies 28 mm in diam. after seven days on MEA; aerial mycelium white; hyphae smooth, simple and clamped; rhizomorphs present; reproductive structures absent; identification based on RFLP analyses using Alu-1 restriction enzyme (Thormann et al. 2001b); widespread; reported from roots of a variety of shrub and tree species (see Shaw III and Kile 1991 for references).

Basidiomycete sp. 1 (ALTA 10853).

From *S. fuscum* (L – 3). Colonies 83 and 74 mm in diam. after seven days on MEA and PDA, respectively, reverse bleached on MEA; aerial mycelium white, patchy, floccose; hyphae hyaline, smooth, 2-4 µm in diam.; clamp connections abundant; conidiophores absent or micronematous; arthroconidia hyaline, various shapes (rectangular, barrel-shaped, curved, edges rounded when mature), abundant, dry, (4.0)-6.0-(16.0) µm x (2.0)-3.0-(4.0) µm; odour sweet; exudate clear to golden-yellow, abundant, among aerial hyphae; isolated on PDA and PDA with benomyl; tannic acid negative, laccase positive.

Basidiomycete sp. 2 (ALTA 10854).

From *S. fuscum* (L – 1), *S. planifolia* leaves (L – 2), *C. aquatilis* leaves (D – 1). Colonies 85 and 80 mm in diam. after seven days on MEA and PDA, respectively, colony reverse not bleached; aerial mycelium white, patchy; hyphae hyaline, smooth, 2.5-4.0 µm in diam.; conidiophores absent or micronematous; arthroconidia hyaline, various shapes (rectangular, barrel-shaped, curved, branched, edges rounded when mature), abundant, dry, (3.0)-4.5-(6.0) µm x (2.0)-2.5-(3.0) µm; isolated on PDA with benomyl, PDA with rose bengal; tannic acid negative, laccase positive, gelatinolytic.

Basidiomycete sp. 3 (ALTA 11312).

From *C. aquatilis* leaves (D – 8). Colonies 85 mm in diam. after seven days on MEA and PDA, reverse bleached on MEA; aerial mycelium white to tan, appressed, thin; hyphae hyaline, smooth, 2.5-5.5 µm in diam.; clamp connections abundant; arthroconidia absent; exudate clear to golden-yellow, abundant, among aerial hyphae; isolated on PDA, PDA with benomyl, PDA with rose bengal; tannic acid negative, laccase positive, gelatinolytic.

Basidiomycete sp. 4 (ALTA 11313).

From *S. planifolia* (D – 2), *C. aquatilis* leaves (D – 7). Colonies 28 and 27 mm in diam. after seven days on MEA and PDA, respectively, reverse bleached on MEA; aerial mycelium white to straw-coloured, floccose; hyphae hyaline, smooth, 1.0-3.0 µm in diam.; clamp connections absent; conidiophores absent or micronematous; arthroconidia hyaline, rectangular, edges rounded when mature, abundant, dry, (3.0)-5.5-(10.0) µm x (1.5)-2.0-(3.5) µm; odour strong, sweet; isolated on PDA, PDA with benomyl, MYC; tannic acid negative, laccase positive.

Basidiomycete sp. 5 (ALTA 11314).

From *C. aquatilis* leaves (D – 1). Colonies 57 mm in diam. after seven days on MEA and PDA, reverse bleached on MEA; aerial mycelium mostly white, raised (crater-like) and patchy, submersed mycelium brown to honey-coloured; hyphae hyaline, smooth, 2.0-3.5 µm in diam.; clamp connections scarce; conidiophores absent or micronematous; arthroconidia hyaline, various shapes (rectangular to barrel-shaped, edges rounded when mature), abundant, dry, (3.0)-4.0-(6.0) µm x (2.0)-2.5-(3.0) µm; isolated on PDA with benomyl; tannic acid negative, laccase positive.

Basidiomycete sp. 6 (ALTA 11315).

From *S. planifolia* leaves (D – 1). Colonies 21 mm in diam. after seven days on MEA and PDA; aerial mycelium white, slightly patchy; hyphae hyaline, smooth, 2.0-3.0 µm in diam.; conidiophores absent or micronematous; arthroconidia hyaline, rectangular, abundant, dry, (3.0)-4.3-(10.0) µm x (1.5)-1.7-(2.0) µm; isolated on PDA, PDA with benomyl; tannic acid negative, laccase positive.

Basidiomycete sp. 7 (ALTA 11316).

From *C. aquatilis* leaves (D – 1). Colonies 54 and 56 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium bright white, patchy to floccose; hyphae hyaline, smooth, 2.0-3.0 µm in diam.; conidiophores absent or micronematous; arthroconidia hyaline, various shapes (rectangular, barrel-shaped, edges rounded when mature), abundant, dry, (3.0)-5.0-(10.0) µm x (2.0)-2.5-(3.0) µm; isolated on PDA with rose bengal; tannic acid positive, laccase positive.

Basidiomycete sp. 8 (ALTA 11317).

From *C. aquatilis* leaves (D – 1). Colonies 55 mm in diam. after seven days on MEA and PDA; aerial mycelium white, patchy; hyphae hyaline, smooth, 2.0-3.0 µm in diam.; conidiophores absent or micronematous; arthroconidia hyaline, barrel-shaped, abundant, dry, (3.0)-4.5-(6.0) µm x (2.0)-2.5-(3.0) µm; isolated on PDA; tannic acid positive, laccase negative.

Bjerkandera adusta (Willd.: Fr.) Karst., 1879, Meddelanden af Societas pro Fauna et Flora Fennica **5**: 38 (ALTA 11712).

From *C. aquatilis* rhizomes (D – 1), *S. fuscum* (L – 1). Mycelium white, cottony-woolly, reverse bleached; arthroconidia hyaline, rectangular, abundant, dry, (5)-9-(13) µm x (2.5)-3.0-(3.5) µm; odour strong, sweet; cosmopolitan; reported from wood (Stalpers 1978); tannic acid positive, laccase positive.

The presence of simple septa, the bleached colony reverse, strong sweet odor, and a positive reaction for laccase separate this basidiomycete from other arthroconidial basidiomycetes (Stalpers 1978) as well as the mycoparasite *Geotrichopsis mycoparasitica* Tzean & Estey (Tzean and Estey 1991).

Fungi Imperfecti

Acremonium butyri (van Beyma) W. Gams, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 126-129 (ALTA 11710).

From *C. aquatilis* leaves (D – 1). Colony yellow-green to olive green, slimy from heavy sporulation; conidia straight to lightly curved, typically cylindrical, (3.0)-5.6-(7.5) µm x (1.5)-2.2-(2.5) µm; widespread; reported from sporocarps of mushrooms, soil, decomposing vegetation (see Gams 1971 for references); weakly pectinolytic (Domsch 1960), weakly lignolytic (Flanagan and Scarborough 1974).

Acremonium chrysogenum (Thisum. & Sukop.) W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 109-111 (ALTA 10669).

From *S. fuscum* (D – 1). Conidia ellipsoidal (2.8)-3.5-(4.1) µm x (1.0)-1.5-(1.9) µm; widespread; reported from soil, decaying vegetation, marine water; cellulolytic, lignolytic, utilizes fats and other carbohydrates (Gams 1971)

Acremonium cf. curvulum W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 57-59 (ALTA 102853, CBS 102853, UAMH 9938).

From *S. fuscum* (D – 3). Colony 13-21 mm in diam. after 10 days on MEA; mycelium mostly submerged and appressed, few white tufts, reverse creamy-yellow to yellow-orange; phialides simple, smooth, no collarette, tapering towards apex, (20)-44-(80) µm; conidia lightly to acutely curved, weakly apiculate at base, rounded at tip, (5.0)-6.3-(8.1) µm x (1.3)-1.9-(2.2) µm; chlamydospores absent; uncommon; reported from soil, water, vegetation (Gams 1971); cellulolytic, utilizes starch.

My isolates differ from *A. curvulum* because mine are slower to sporulate, have scant aerial mycelium, and less intense orange colouration of the medium. Conidial and phialidic dimensions and growth rates are close to *A. curvulum*. My isolates were used in a study on the cell wall degradation of *S. fuscum* (Tsuneda et al. 2001).

Acremonium egyptiacum (van Beyma) W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 64-65 (ALTA 11711).

From *C. aquatilis* leaves (L – 1). Colony faint pink; conidia in chains, rounded tip and apiculate at base, (3.0)-5.3-(6.5) µm x (1.0)-1.3-(1.5) µm; common; reported from soil, root, cereal seeds (see Gams 1971 for references).

Acremonium state of *Nectria rishbethii* Booth, 1959, Mycological Papers **73**: 92 (ALTA 11714).

From *S. planifolia* leaves (L – 1), *C. aquatilis* leaves (D – 1). Colony reverse dark orange-brown on PDA; conidia straight to slightly curved, (3.4)-4.2-(5.0) µm x (1.0)-1.4-(2.0) µm; uncommon; reported from wood (Gams 1971).

Acremonium strictum W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 42-44 (ALTA 10670).

From *C. aquatilis* rhizomes (D – 1) and leaves (D – 2), *S. planifolia* roots (L – 1), *S. fuscum* (D – 1). Conidia cylindrical, (4.0)-4.4-(5.7) µm x (0.9)-1.5-(2.0) µm; cosmopolitan; reported from soil, vegetation, wood, fungi, dung, jet fuel, aquatic habitats, human tissues, and air (see Domsch et al. 1980 for references); cellulolytic, gelatinolytic.

Alternaria alternata (Fr.) Keissler, 1912, Beihefte zum Botanischen Zentralblatt **29**: 434 (ALTA 10671).

From *C. aquatilis* leaves (L – 1), *S. planifolia* leaves (L – 5, D – 4). Conidia in long chains, each with a short beak (less than one third of length of conidium), (23)-32-(42) µm x (12)-13-(15) µm; cosmopolitan; reported from soil, plants, foods, textiles (see Domsch et al. 1980 for references); pectinolytic (Wieringa 1956), cellulolytic (Lizak 1975), lignolytic (Fischer 1953), utilizes variety of carbohydrates (Franz 1975).

Arthrinium state of *Apiospora montagnei* Sacc., 1875, Nuovo Giornale Botanico Italiano **7**: 306 (ALTA 10672).

From *C. aquatilis* rhizomes (D – 1), *S. planifolia* leaves (D – 3). Conidia pale brown, lenticular, hyaline germ slit, (5.5)-6.7-(7.5) µm; conidiophores hyaline, thin, few septate, 0.5-0.8 µm; widespread; reported from soil, variety of herbaceous plant species, wood, feces, human tissues (see Domsch et al. 1980 for references); possibly cellulolytic (Ionita 1973).

Aspergillus niger v. Tiegh., 1867, Annales des Sciences Naturelles. A. Botanique, Séries 5, **8**: 240 (ALTA 10673).

From *S. fuscum* (L – 2, D – 1). Conidia globose, verrucose, (3.5)-4.8-(5.4) µm; cosmopolitan; reported from soil, animals, human tissues, foods, decaying vegetation, and air (see Domsch et al. 1980 and Klich and Pitt 1994 for references); utilizes a variety of substrates, including chitin (Kawasaki and Ito 1964) and starch (Barton et al. 1972).

Aspergillus versicolor (Vuill.) Tiraboschi, 1908/09, Annali di Botanica, Roma **7**: 9 (ALTA 10674).

From *S. fuscum* (D – 1). Conidia globose, echinulate, (2.2)-2.7-(3.0) µm; cosmopolitan; reported from soil, vegetation, animals, water, and foods (see Domsch et al. 1980 for references); weakly cellulolytic (Reese and Downing 1951), utilizes starch (Franz 1975) and other carbohydrates (Trique 1968).

Aureobasidium pullulans (de Bary) Arn., 1910, Annales of Mycology **8**: 475 (ALTA 10675).

From *C. aquatilis* (L – 4), *S. planifolia* leaves (L – 13). Hyphae hyaline when young, melanized when mature; conidia hyaline, ellipsoidal, conidiogenesis synchronous, (5.5)-6.8-(8.0) µm x (2.0)-2.6-(3.0) µm; cosmopolitan; reported from soil, living and decomposing vegetation, sewage, freshwater and marine water (see Domsch et al. 1980 for references); pectinolytic (Loub 1960), cellulolytic (Berndt and Liese 1971), lignolytic (Henderson 1963).

Botrytis cinerea Pers. *ex* Pers., 1822, Synopsis Methodica Fungorum, p. 690 (ALTA 10676).

From *C. aquatilis* leaves (L – 3, D – 2), *S. planifolia* leaves (L – 3, D – 3), *S. fuscum* (D – 1). Macroconidia pale brown, obovoid, smooth-walled, often with protuberant hilum, (10)-11-(13) µm x (5)-6-(7) µm, microconidia globose, (2.4)-2.8-(3.2) µm; cosmopolitan; reported from vegetation, animal tissues, air, and soil (see Domsch et al. 1980 for references); cellulolytic (Basu and Ghose 1960), pectinolytic (Domsch and Gams 1969).

Cladosporium cladosporioides (Fres.) de Vries, 1952, Contribution to the Knowledge of the Genus *Cladosporium* Link *ex* Fries, p. 57 (ALTA 10677).

From *C. aquatilis* leaves (L – 9), *S. planifolia* leaves (L – 4, D – 1). Conidiophores acropleurogenously branched; conidia ellipsoidal to limoniform, smooth to finely verruculose, (4.5)-5.2-(6.2) µm x (2.5)-2.7-(3.0) µm; cosmopolitan; reported from vegetation, soil, water, feces, and food (see Domsch et al. 1980 for references); weakly cellulolytic and lignolytic (Flanagan and Scarborough 1974).

Cladosporium herbarum (Pers.) Link *ex* Gray, 1821, Natural Arrangement of British Plants I, p. 556 (ALTA 10678).

From *C. aquatilis* leaves (L – 14, D – 2), *S. planifolia* roots (D – 2) and leaves (L – 18, D – 10), *S. fuscum* (L – 1). Conidia ellipsoidal to cylindrical, sometimes one-septate, verruculose, scars prominent, (2)-8-(16) µm x (2)-3-(4) µm; cosmopolitan; reported from vegetation, soil, aquatic habitats, dung, animal tissues, air, and food (see Domsch et al. 1980 for references); cellulolytic (Marsh et al. 1949), pectinolytic (Domsch and Gams 1969), utilizes starch (Domsch 1960).

Cladosporium murorum (Pers.) Petr., 1941, Annalen des Naturhistorischen Museums, Wien, **52**: 288 (ALTA 12285).

From *C. aquatilis* leaves (L – 1). Conidiophores with terminal or intercalary swellings; conidia ellipsoidal to cylindrical, always non-septate, verruculose, (2)-8-(16) µm x (2)-3-(4) µm; cosmopolitan; reported from vegetation, soil, air, and food (see Domsch et al. 1980 for references)

Dimorphospora foliicola Tubaki, 1958, Journal of the Hattori Botanical Laboratory **20**: 156-158 (ALTA 11713).

From *C. aquatilis* leaves (D – 7), *S. planifolia* leaves (D – 10). Macroconidia long ovoid to reniform, (12)-14-(16) µm x (6)-7-(8) µm, microconidia subglobose, (2.0)-2.2-(3.0) µm x (1.5)-2.1-(2.5) µm; common; reported from decaying leaf litters (Abdullah et al. 1981).

Epicoccum purpurascens Ehrenb. *ex* Schlecht., 1824, Synopsis of Plants and Cryptogams, p. 136 (ALTA 10679).

From *C. aquatilis* leaves (L – 1). Conidia golden-brown to brown, globose to pyriform, funnel-shaped at base and having a broad seceding scar, (18)-20-(23) µm; cosmopolitan; reported from soil, animal and human tissues (see Domsch et al. 1980 for references); cellulolytic (Domsch 1960), pectinolytic (Hamilton and Johnston 1961), utilizes a variety of additional carbohydrates (Domsch and Gams 1969).

Fusarium aquaeductuum var. *medium* Wollenw., 1931, Fusarium-Monographie: Fungi Parasitici et Saprophytici, p. 556 (ALTA 10680).

From *C. aquatilis* rhizomes (L – 1), *S. fuscum* (L – 1). Phialides simple to basitonously branched; macroconidia curved to (sometimes) straight, (usually) tri-septate, (38)-44-(52) µm x (3.8)-4.3-(5.0) µm; microconidia ellipsoidal to slightly curved, (sometimes) septate, (6)-7-(10) µm x (1.5)-1.8-(2.0) µm; cosmopolitan; reported from water, sewage, fungi, peat (see Domsch et al. 1980 for references); cellulolytic (Gersonde and Kerner-Gang 1968), utilizes polyphenolics (Barz et al. 1976).

Fusarium chlamydosporum Wollenw. & Reink., 1925, Die Fusarien, p. 89 (ALTA 10681).

From *S. planifolia* roots (D – 2). Phialides with numerous sympodial branches; macroconidia slightly curved, (usually) tri-septate, with a foot cell, (24)-29-(37) µm x (2.5)-3.0-(3.5) µm, microconidia fusiform to elongate, (sometimes) septate, (6.5)-10-(12) µm x (1.8)-2.4-(3.0) µm; cosmopolitan; reported from soil, wood, roots, fruit (see Domsch et al. 1980 for references).

Fusarium oxysporum Schlecht., 1824, Flora Berlin **3**: 10 (ALTA 10682).

From *C. aquatilis* rhizomes (L – 1). Phialides simple to basitonously branched; macroconidia curved, (usually) tri-septate, basal foot cell, (35)-40-(50) µm x (3.0)-3.1-(3.5) µm, microconidia ellipsoidal to cylindrical, may be slightly curved, (usually) non-septate, (6)-8-(10) µm x (2.0)-2.5-(3.0) µm; chlamydospores terminal; cosmopolitan; reported from soil and plants (see Domsch et al. 1980 for references); pectinolytic (Domsch and Gams 1969), cellulolytic (Barz 1971), lignolytic, utilizes variety of other carbohydrates (Ross 1960).

Fusarium sporotrichioides Sherb., 1915, Memoirs. Cornell University Agricultural Experimental Station **6**: 183-186 (ALTA 10683).

From *S. planifolia* roots (D – 2). Phialides abundantly branched; macroconidia curved, (usually) tri-septate, with inconspicuous foot cell, (23)-26-(34) µm x (2.9)-3.0-(3.2) µm, microconidia fusiform to pyriform, (usually) non-septate, (6.5)-11-(15) µm x (2.0)-3.5-(6.0) µm; chlamydospores intercalary, often in series; cosmopolitan; reported from soil and plants (see Domsch et al. 1980 for references); cellulolytic (Went and de Jong 1966), utilizes a variety of other carbohydrates (Kvashnina 1976).

Hormonema dematioides Lagerb. & Melin, 1927, Svenska Skogsvardsfören Tidskrift **2-4**: 233 (ALTA 10684).

From *C. aquatilis* (L – 1), *S. planifolia* leaves (L – 4). Hyphae thin and hyaline when young, thickened and melanized when mature; conidia hyaline, ellipsoidal, basipetal conidiogenesis, (5.0)-9.1-(14.0) µm x (2.0)-2.5-(3.1) µm; cosmopolitan; reported from plants (Hermanides-Nijhof 1977).

Monocillium constrictum W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), p. 164-165 (ALTA 10685).

From *C. aquatilis* leaves (D – 13), *S. fuscum* (L – 1). Colony faint orange to ochre; phialides simple, densely arranged along hyphae, (8)-11-(19) µm; conidia slightly curved, rounded apex and apiculate at base, (4)-5-(6) µm x (1.0)-1.4-(1.7) µm; cosmopolitan; reported from plants, air, fungal sporocarps (see Gams 1971 for references); cellulolytic, gelatinolytic, utilizes tannic acid and starch.

Monocillium nordinii (Bourchier) W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), p. 162-163 (ALTA 12286).

From *C. aquatilis* leaves (D - 3), *S. planifolia* roots (L – 1, D - 1). Colony faint orange to pink; phialides simple, densely arranged along hyphae, often with swollen apex, (23)-33-(45)

µm; conidia hyaline, ovoid to ellipsoid, (2.5)-3.6-(5.0) µm x (1.0)-1.5-(2.0) µm; chlamydospores globose, intercalary; common; reported from wood, fungal rhizomorphs (Gams 1971).

Nodulisporium sp. (ALTA 10698).

From *C. aquatilis* leaves (L – 1, D - 3), *S. planifolia* leaves (D – 2), *S. fuscum* (L – 1, D – 1). Colony 20 mm in diam. after seven days on MEA, greyish-brown, velvety towards margin; conidiophores branched, (46)-118-(259) µm; conidiogenous cells (12)-18-(24) µm; conidia pale brown, ellipsoidal to obovoid, truncate, solitary, dry, (3.2)-3.8-(4.1) µm x (1.3)-1.7-(2.1) µm; cosmopolitan; reported from herbaceous plants, wood, decomposing plant materials (Ellis 1971, Deighton 1985); cellulolytic, gelatinolytic, utilizes starch.

Oidiodendron maius Barron, 1962, Canadian Journal of Botany **40**: 600-602 (ALTA 10700, UAMH 9749).

From *S. fuscum* (D – 1). Conidiophores (150)-260-(350) µm x (1.8)-2.8-(3.8) µm; arthroconidia hyaline, (3.0)-3.6-(4.0) µm x (1.9)-2.1-(2.2) µm; cosmopolitan; reported from soil, roots of Ericaceae (see Hambleton and Currah 1997 for references); cellulolytic, gelatinolytic, utilizes starch and tannic acid.

This isolate was used in a study on the cell wall degradation of *S. fuscum* (Tsuneda et al. 2001).

Oidiodendron scytaloides Gams & Söderström, 1983, Cryptogamie, Mycologie **4**: 239-241 (UAMH 9750, 9751).

From *S. fuscum* (L – 2, D - 1). Conidiophores (35)-75-(225) µm; arthroconidia hyaline, (2.0)-3.1-(4.0) µm x (1.3)-1.6-(1.7) µm; chlamydospores dark, ellipsoidal, finely verrucose, in terminal and intercalary series, (3.2)-4.1-(6.0) µm x (2.0)-2.9-(4.8) µm; cosmopolitan; reported from conifer forest soils (Gams and Söderström 1983); gelatinolytic, pectinolytic, utilizes starch, tannic acid.

Paecilomyces marquandii (Massee) Hughes, 1951, Mycological Papers **45**: 30 (ALTA 10855).

From *S. fuscum* (L – 1). Diffusible yellow exudate on MEA; phialides swollen at base with long, tapering neck, (9)-11-(12) µm; conidia ellipsoidal to fusiform, in chains, (3.0)-3.6-(4.3) µm x (1.8)-2.1-(2.5) µm; cosmopolitan; reported from soil (see Domsch et al. 1980 for references); gelatinolytic (Borut 1960), chitinolytic (Jackson 1965), utilizes starch (Franz 1975).

Penicillium chrysogenum Thom, 1910, Bulletin. Bureau of Animal Industry. U.S. Department of Agriculture **118**: 58, (ALTA 12288).

From *C. aquatilis* rhizomes (D – 1) and leaves (L – 4, D –4), *S. planifolia* roots (L – 1). Conidiophores terverticillate, (195)-240-(290) µm; phialides ampulliform, (4)-6-(9) µm; conidia spherical to ellipsoidal, (3.2)-3.7-(4.1) µm long; cosmopolitan; reported from soil, vegetation, food (Pitt 1988); pectinolytic (Takagawa 1939), utilizes various sugars (Vinze 1962) and starch (Bodnarchuk 1964), cellulolytic, gelatinolytic.

Penicillium funiculosum Thom, 1910, Bulletin. Bureau of Animal Industry. U.S. Department of Agriculture **118**: 69 (ALTA 10856).

From *C. aquatilis* rhizomes (L – 1, D – 4) and leaves (L – 2, D – 4), *S. planifolia* roots (L – 1) and leaves (D – 2), *S. fuscum* (L – 9, D – 4). Conidiophores biverticillate, (59)-74-(140) µm; phialides acerose, (9)-11-(12) µm; conidia ellipsoidal to spherical, (2.5)-2.9-(3.4) µm long; cosmopolitan; reported from soil (Pitt 1988); cellulolytic (Gochenaur 1975), utilizes various sugars (Dickinson and Boardman 1970).

Penicillium montanense Christensen & Backus, 1962, Mycologia **54**: 574 (ALTA 10858).

From *S. fuscum* (D – 2). Conidiophores monoverticillate, distinctly vesiculate, (150)-180-(240) µm; phialides ampulliform, (9)-11-(12) µm; conidia greyish turquoise, spherical, distinctly spinose, (3.2)-3.6-(4.1) µm; uncommon; reported from cultivated soils (Pitt 1988).

Penicillium odoratum Christensen & Backus, 1961, Mycologia **53**: 459-462 (ALTA 10857).

From *C. aquatilis* leaves (D – 1), *S. fuscum* (D – 4). Conidiophores monoverticillate, distinctly vesiculate, (150)-180-(240) µm; phialides ampulliform, (7)-9-(10) µm; conidia blue, broadly ellipsoidal, distinctly rough-walled, (3.3)-3.8-(4.1) µm long; cosmopolitan; reported from peatlands, undisturbed forest soils (Christensen and Backus 1961, Pitt 1988); cellulolytic (Franz and Loub 1959), pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Penicillium purpurogenum Stoll, 1904, Beiträge zur Charakterisierung von *Penicillium* **32** (ALTA 10859).

From *C. aquatilis* rhizomes (L – 1), *S. fuscum* (L – 5). Red pigmentation on Czapek's Yeast Extract agar; conidiophores biverticillate, (95)-210-(295) µm; phialides ampulliform, (8)-

10-(12) μm; conidia ellipsoidal, rough-walled, (2.9)-3.2-(3.5) μm long; cosmopolitan; reported from soil (Pitt 1988); cellulolytic, pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Penicillium spinulosum Thom, 1910, Bulletin. Bureau of Animal Industry. U.S. Department of Agriculture **118**: 76.

From *C. aquatilis* leaves (L – 1). Conidiophores monoverticillate, vesiculate, (150)-232-(310) μm; phialides ampulliform, (6)-8-(9) μm; conidia spherical, distinctly spiny, (2.9)-3.2-(3.5) μm; cosmopolitan; reported from soil, vegetation, food, textiles (Pitt 1988); cellulolytic, pectinolytic (Heinen 1962).

Penicillium thomii Maire, 1910, Bulletin. Societé d'Histoire Naturelle de l'Afrique du Nord **8**: 189 (ALTA 10860).

From *C. aquatilis* rhizomes (D – 2) and leaves (D – 1), *S. planifolia* leaves (L – 1), *S. fuscum* (L – 4, D – 19). Conidiophores monoverticillate, distinctly vesiculate, (280)-310-(370) μm; phialides ampulliform, (8)-10-(12) μm long; conidia sub-spherical to ellipsoidal, rough-walled, (3.5)-4.0-(4.5) μm; cosmopolitan; reported from decaying vegetation, foods, fungi, soil (Pitt 1988); cellulolytic (Jefferys et al. 1953), pectinolytic (Flanagan and Scarborough 1974), gelatinolytic, utilizes starch.

Penicillium verruculosum Peyronel, 1913, I Germi Atmosferici dei Funghi con Micelio 22.

From *C. aquatilis* leaves (L – 1). Conidiophores biverticillate, (130)-188-(230) μm; phialides ampulliform to acerose, (6)-8-(10) μm; conidia spherical, rough-walled, (2.9)-3.3-(3.6) μm; cosmopolitan; reported from soil (Pitt 1988).

Phialocephala dimorphospora Kendrick, 1961, Canadian Journal of Botany **39**: 1080-1083 (ALTA 10861, 10701).

From *C. aquatilis* rhizomes (L – 4, D – 10), *S. planifolia* roots (L – 1, D – 4) and leaves (D – 1). Conidiophores smooth; phialides pale brown, collarette distinct, (7)-9-(12) μm; conidia hyaline, abundant, two types, globose, (1.8)-2.0-(2.2) μm and ovoid, (3.5)-3.7-(4.0) μm x (1.9)-2.0-(2.1) μm; widespread; reported from decomposing wood (Kendrick 1961); cellulolytic, gelatinolytic, utilizes starch.

Phialocephala fortinii Wang & Wilcox, 1985, Mycologia 77: 954-956 (ALTA 10702).

From *C. aquatilis* rhizomes (L – 3, D –2), *S. planifolia* roots (L – 2, D - 9). Conidiophores verrucose; phialides pale brown, collarette distinct, (8)-9-(15) µm; conidia hyaline, globose, uncommon, (1.5)-1.7-(2.0) µm; widespread; reported from roots of a wide range of herbaceous and woody plant species (Sigler and Flis 1998); lignolytic, laccase positive (Currah and Tsuneda 1993).

Phialophora alba van Beyma, 1943, Antonie van Leeuwenhoek 9: 56 (ALTA 11715).

From *C. aquatilis* rhizomes (L – 2, D – 2) and leaves (D – 7), *S. planifolia* roots (L – 3, D - 14) and leaves (L – 1, D –10). Phialides simple or in *Penicillium*-like heads; collarette inconspicuous; conidia subglobose to ovoid, (2.5)-3.1-(4.0) µm x (2.0)-2.6-(3.0) µm; common; reported from soil (Schol-Schwarz 1970).

Phialophora cf. alba (ALTA 12287, UAMH 9929).

From *C. aquatilis* rhizomes (L – 6, D – 53) and leaves(D – 11), *S. planifolia* roots (D – 1) and leaves (D – 4). Colonies 34 mm diam. after seven days on MEA, cream-coloured, aerial mycelium scant, moist appearance; colonies become orange-red to reddish-brown with age on PDA; aerial mycelium white to tan; conidiophores smooth, walls parallel, hyaline, (10)-17-(25) µm; phialides in penicillate arrangement, 1-3 metulae, sometimes distended at base, smooth, (8.0)-8.8-(12.0) µm x (3.0)-3.2-(3.5) µm; collarette deep, walls parallel, often two conidia contained within collarette, hyaline, (4.0)-4.5-(5.0) µm x (2.5)-3.1-(3.5) µm; conidia globose to oblong, hyaline, in slimy heads, produced in large quantities, (2.5)-2.9-(3.5) µm x (2.0)-2.3-(2.5) µm; isolated on PDA, PDA with benomyl, PDA with rose bengal, and MYC.

My isolates are similar to *P. alba* in colony and phialide characteristics; however, they differ substantially from *P. alba* in forming solitary, lateral conidia that appear to be indehiscent (*cf.* chlamydospores), in the formation of well-developed, penicillately-branched conidiophores, in having deep collarettes containing up to two conidia, and in producing larger conidia.

Phialophora cyclaminis van Beyma, 1942, Antonie van Leewenhoek 8: 115 (ALTA 11716).

From *S. planifolia* roots (L – 1). Phialides pale brown, simple, (6)-9-(13) µm x (3.0)-3.4-(4.0) µm; collarette distinct; conidia hyaline, spherical, (1.8)-2.1-(2.4) µm; uncommon; reported from wood, water, leaves (Schol-Schwarz 1970).

Phialophora malorum (Kidd & Beaum.) McColloch, 1944, Mycologia **36**: 589 (ALTA 11717, UAMH 9862).

From *C. aquatilis* rhizomes (L – 1). Phialides pale brown, simple or branched, (12)-18-(24) µm x (3.0)-4.0-(5.0) µm; collarette indistinct; conidia hyaline, ellipsoidal to cylindrical, in heads, (5.0)-5.3-(6.0) µm x (1.0)-1.9-(2.5) µm; widespread; reported from soil, wood, decaying fruit, animals, water (see Domsch et al. 1980 and Schol-Schwarz 1970 for references).

Phialophora melinii (Nannf.) Conant, 1937, Mycologia **29**: 598 (ALTA 11718).

From *S. planifolia* roots (D – 1). Phialides pale brown, simple, (10)-14-(18) µm; collarette distinct; conidia hyaline, ovoid to ellipsoidal, in slimy heads, (3.0)-3.5-(4.0) µm x (1.0)-1.6-(1.9) µm; widespread; reported from wood and wood pulp (Cole and Kendrick 1973).

Polyscytalum cf. hareae (ALTA 10862).

From *S. planifolia* roots (D – 1) and leaves (D – 4). Colony 11 mm in diam. after seven days on MEA; aerial mycelium pale brown to olive-brown; exudate clear; conidia cylindrical, smooth, septate, ends truncate, chains break up readily, (15)-19-(24) µm x (1.8)-2.0-(2.2) µm.

Polyscytalum hareae (Sutton) Kirk (1981, Transactions of the British Mycological Society **76**: 81-82) has been reported from decomposing *Eucalyptus* spp. (Kirk 1981) and *Phragmites communis* leaves (Apinis et al. 1972).

Pycnidial sp. 1 (ALTA 12289).

From *C. aquatilis* rhizomes (D – 1). Colony 25 mm in diam. after seven days on MEA; aerial mycelium hyaline, scant, submersed mycelium hyaline to pale brown, reverse fuscous to olivaceous; hyphae hyaline, septate, smooth, 2-3 µm in diam.; pycnidia dematiaceous, globose, (65)-190-(270) µm; conidia hyaline, single-celled, biguttulate, straight to slightly curved, (4.2)-4.7-(5.0) µm x (1.0)-1.2-(1.5) µm; isolated on PDA with benomyl.

Pycnidial sp. 2 (ALTA 12290).

From *C. aquatilis* rhizomes (D – 3). Colony 80 mm in diam. after seven days on MEA; aerial mycelium hyaline, scant to absent, submersed mycelium hyaline; hyphae hyaline, septate, smooth, 2-3 µm in diam.; pycnidia dematiaceous, globose, (350)-900-(1,300) µm; conidia hyaline, single-celled, slightly curved to falcate, (3.5)-3.9-(4.1) µm x (0.8)-0.9-(1.1) µm; isolated on PDA and PDA with benomyl.

Pycnidial sp. 3 (ALTA 12291).

From *S. planifolia* roots (L – 1). Colony 24 mm in diam. after seven days on MEA; aerial mycelium hyaline, scant, submersed mycelium tan to pale brown; hyphae hyaline, septate, smooth, 2-3 µm in diam.; pycnidia dematiaceous, globose, (350)-900-(1,300) µm; conidia hyaline, single-celled, falcate, apex apiculated, (7.5)-8.0-(9.0) µm x (1.1)-1.4-(1.5) µm; isolated on PDA with benomyl.

Pycnidial sp. 4 (ALTA 12292).

From *S. planifolia* roots (L – 1). Colony 34 mm in diam. after seven days on MEA; aerial mycelium hyaline to tan, scant, submersed mycelium dematiaceous; hyphae dematiaceous, septate, smooth, 2-3 µm in diam.; pycnidia dematiaceous, globose, (190)-380-(500) µm; conidia hyaline, single-celled, biguttulate, straight to slightly curved, (3.5)-4.3-(5.0) µm x (1.4)-1.5-(1.7) µm; isolated on PDA.

Pycnidial sp. 5 (ALTA 12293).

From *C. aquatilis* rhizomes (D – 1). Colony 31 mm in diam. after seven days on MEA; aerial mycelium hyaline, scant to absent, submersed mycelium hyaline; hyphae hyaline, septate, smooth, 2-3 µm in diam.; pycnidia hyaline to light tan, globose, (100)-145-(200) µm; conidia hyaline, single-celled, globose to limoniform, (6.0)-7.1-(8.0) µm x (4.0)-4.6-(5.0) µm; isolated on PDA.

Pycnidial sp. 6 (ALTA 12294).

From *S. planifolia* roots (D – 1). Colony 70 mm in diam. after seven days on MEA; aerial mycelium hyaline, scant to absent, submersed mycelium hyaline; hyphae hyaline, septate, smooth, 2-3 µm in diam.; pycnidia dematiaceous, globose, (300)-1,000-(1,500) µm; conidia hyaline, single-celled, straight to slightly curved, (4.5)-5.0-(5.5) µm x (1.0)-1.3-(1.5) µm; isolated on PDA.

Pycnidial sp. 7 (ALTA 12295).

From *S. planifolia* roots (D – 1). Colony 72 mm in diam. after seven days on MEA; aerial mycelium hyaline, scant to absent, submersed mycelium hyaline; hyphae hyaline, septate, smooth, 2-3 µm in diam.; pycnidia dematiaceous, globose, (230)-450-(600) µm; conidia hyaline, single-celled, straight to slightly curved, (3.8)-4.4-(5.0) µm x (1.0)-1.1-(1.5) µm; isolated on PDA.

Scopulariopsis brevicaulis (Sacc.) Bain., 1907, Bulletin. Societé Mycologique de France **23**: 99 (ALTA 10704).

From *S. planifolia* leaves (D – 1). Conidiophores cylindrical, verticillately branched, (12)-18-(21) µm; conidia globose to ovoid, coarsely verrucose, (5.0)-6.7-(7.5) µm; cosmopolitan; reported from soil, vegetation, water, animals (see Domsch et al. 1980 for references); cellulolytic, pectinolytic, lignolytic, chitinolytic, utilizes starch (Tubaki 1958).

Sporothrix state of *Ophiostoma stenoceras* (Robak) Melin & Nannf., 1932, Svenska Skogsvardsforeningens Tidskrift **32**: 408 (ALTA 11311, UAMH 9753).

From *S. fuscum* (D – 3). Conidiogenous cells simple, erect, (22)-30-(43) µm, with an inconspicuous conidiiferous denticle at apex; conidia hyaline, ovoid to fusiform, (3.2)-4.4-(5.2) µm x (1.1)-1.5-(1.9) µm; ascogenous state immature; cosmopolitan; reported from human tissues, wood, herbaceous plants, soil (de Hoog 1974); pectinolytic, utilizes tannic acid and starch.

Sporothrix sp. 1 (UAMH 9752).

From *S. fuscum* (D – 4). Colony 5 mm in diam. after seven days on MEA; mycelium hyaline when young, becoming purplish to black after 10 days on MEA, mycelium purple on cereal agar; conidiogenous cells simple, erect, (3)-7-(15) µm; conidiiferous denticle at apex, 2-3 µm wide; conidia hyaline, ovoid to fusiform, single-celled, contain large oil body, (2.0)-2.8-(3.2) µm x (1.3)-1.8-(2.0) µm, blastoconidia pale brown, globose, abundant, laterally produced, (1.5)-2.5-(3.2) µm; the genus is reported from soil, plants, humans tissues, decomposing vegetation (de Hoog 1974); isolated on MYC; gelatinolytic, unable to utilize tannic acid, starch, or pectin.

Sporothrix sp. 2 (ALTA 12296, UAMH 9930).

From *S. planifolia* roots (L – 1). Colony 10 mm in diam. after seven days on MEA, diffusible brown pigment on cereal agar; mycelium hyaline when young, becoming purplish to black after 10 days on MEA, mycelium purple on cereal agar; conidiogenous cells simple, erect, tapering towards apex, thin-walled, (5)-14-(27) µm; conidia hyaline, globose to subglobose, single-celled, borne on pedicels at apex and laterally on phialides, (1.8)-2.4-(3.0) µm x (1.6)-1.9-

(2.2) µm, blastoconidia pale brown, globose, abundant, lateral, thick-walled, (2.9)-3.0-(3.1) µm; isolated on MYC.

Stagonospora caricis (Oud.) Sacc., 1884, Sylloge Fungorum **3**: 452 (ALTA 12297).

From *C. aquatilis* leaves (L – 2). Pycnidia dematiaceous, globose, immersed, (135)-175-(200) µm; conidia 3-7 septate, constricted, straight to slightly curved, basal foot cell, (31)-37-(46) µm x (4.0)-4.5-(5.0) µm; widespread; reported from leaves of *Carex* spp. (Sutton 1980).

Stagonospora sp. 1 (ALTA 12298).

From *S. planifolia* leaves (L – 1). Colony 30 mm in diam. after seven days on MEA; aerial mycelium tan, scant; hyphae smooth, septate, 3-4 µm in diam.; pycnidia dematiaceous, globose, immersed, (110)-155-(190) µm; conidia 3-6 septate, constricted, straight to slightly curved, (40)-51-(58) µm x (3.0)-4.0-(5.0) µm; widespread; reported from leaves of herbaceous plants (Sutton 1980).

Trichoderma aureoviride Rifai, 1969, Mycological Papers **116**: 34-38 (ALTA 10707).

From *C. aquatilis* rhizomes (D – 1), *S. planifolia* roots (D – 1) and leaves (D - 3), *S. fuscum* (D – 2). Colony reverse golden to golden-yellow due to needle-shaped crystals in medium; conidia obovoid, smooth, (2.2)-3.9-(4.4) µm x (1.9)-2.6-(3.1) µm; cosmopolitan; reported from soil, vegetation, cork (see Rifai 1969 for references); cellulolytic, gelatinolytic, utilizes starch.

Trichoderma harzianum Rifai, 1969, Mycological Papers **116**: 38-42 (ALTA 10708).

From *C. aquatilis* rhizomes (D – 1) and leaves (L – 2, D – 9), *S. planifolia* roots (L – 4, D – 3) and leaves (D – 10), *S. fuscum* (L – 1, D – 2). Conidia subglobose to oval, smooth, (2.2)-2.5-(3.0) µm; cosmopolitan; reported from soil, vegetation, paper, textiles, and jet fuel (see Domsch et al. 1980 for references); cellulolytic (Park 1976), utilizes starch (Franz 1975), gelatinolytic, pectinolytic.

Trichoderma koningii Oud., 1902, Archives Neerlandaise des Sciences Extactes et Naturelles, Séries **7**: 291 (ALTA 10709).

From *S. planifolia* roots (L – 2, D – 6) and leaves (L - 1), *C. aquatilis* rhizomes (D – 5) and leaves (L – 2). Phialides arranged in complex manner, (7.7)-9.2-(11.5) x (2.7)-3.4-(3.7) µm;

conidia pale-green to green, elliptical to sub-cylindrical, smooth, (2.8)-3.6-(4.3) x (1.9)-2.3-(2.9) µm; cosmopolitan; reported from soil, leaf litter (see Domsch et al. 1980 for references); cellulolytic, pectinolytic (Fanelli and Cervone 1977), lignolytic (Ceruti Scurti et al. 1972), chitinolytic (Butzke et al. 1972), utilizes starch (Toyama 1960).

Trichoderma piluliferum Webster & Rifai, 1969, Mycological Papers **116**: 16-18 (ALTA 10711).

From *C. aquatilis* rhizomes (D – 1), *S. planifolia* roots (L – 2, D - 6) and leaves (D – 3). Mycelium white; phialides short and plump, (4.7)-5.8-(6.7) x (2.6)-3.4-(3.7) µm; conidia hyaline, globose, smooth, (2.2)-3.0-(3.6) µm; cosmopolitan; reported from wood (Rifai 1969).

Trichoderma polysporum (Link *ex* Pers.) Rifai, 1969, Mycological Papers **116**: 18-22 (ALTA 10712).

From *C. aquatilis* rhizomes (D – 4) and leaves (L – 1), *S. planifolia* roots (L – 4, D –7), *S. fuscum* (D – 2). Mycelium white, sterile hyphae extend beyond phialide apices; phialides short and plump, (3.9)-5.1-(6.0) x (2.9)-3.5-(4.2) µm; conidia hyaline, ellipsoidal, smooth, (3.3)-3.6-(4.0) x (1.4)-1.8-(2.1) µm; cosmopolitan; reported from soils, plant litter, rhizosphere of plants (see Domsch et al. 1980 for references); cellulolytic (Park 1976), weakly chitinolytic (Jackson 1965), utilizes variety of sugars (Danielson and Davey 1973).

Trichoderma pseudokoningii Rifai, 1969, Mycological Papers **116**: 45-47 (ALTA 10710).

From *C. aquatilis* rhizomes (D – 2), *S. planifolia* roots (L – 4, D – 3) and leaves (D – 2). Phialides arranged often singly along hyphae, (5.7)-6.9-(8.5) x (2.4)-3.2-(3.6) µm; conidia pale-green to green, elliptical to sub-cylindrical, smooth, (3.6)-4.0-(4.5) x (1.8)-2.2-(2.4) µm; uncommon; reported from wood (Rifai 1969).

Trichoderma viride Pers. *ex* Gray, 1821, Natural Arrangement of British Plants I, p. 560 (ALTA 10713).

From *C. aquatilis* rhizomes (L – 2, D - 2) and leaves (L – 2, D - 2), *S. planifolia* roots (L – 1, D – 17) and leaves (L – 1, D – 10), *S. fuscum* (L – 4, D – 12). Conidia green, globose, verrucose, (3.2)-3.7-(4.1) µm; cosmopolitan; reported from soil, aquatic ecosystems, vegetation, dung, food, animal tissues (see Domsch et al. 1980 for references); cellulolytic (Reese and Levinson 1952), pectinolytic (Domsch and Gams 1969), chitinolytic (Domsch 1960), gelatinolytic, utilizes starch.

Ulocladium botrytis Preuss, 1851, Linnaea 24: 111 (ALTA 10714).

From *S. planifolia* leaves (D – 1). Conidia golden-brown, broadly ellipsoidal to ovoid, verrucose, solitary, up to three transverse septa and one longitudinal septum, (18)-22-(25) µm x (9)-10-(11) µm; cosmopolitan; reported from soil, wood, paper, textiles, decomposing herbaceous plants (Ellis 1971).

Verticillium balanoides (Drechsler) Dowsett, Reid & Hopkin, 1982, Mycologia 74: 687-690 (ALTA 12299, UAMH 9931).

From *S. planifolia* roots (L – 2, D - 1) and leaves (D – 1). Conidiophores tapering towards apex, sometimes branched, (25)-57-(80) µm; phialides swollen at base (3-5 µm), tapering towards apex, 4-8 phialides per verticil, (10)-12-(14) µm; conidia hyaline, globose to irregularly-shaped, in slimy heads, (1.6)-1.9-(2.2) µm; reported from nematodes, soil (Dowsett et al. 1982).

Verticillium bulbillosum W. Gams & Malla, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 189-190 (ALTA 10715).

From *S. fuscum* (L – 2, D - 7). Conidia curved, in slimy heads at apex of phialide, length variable, primary conidia often longer and more curved than secondary conidia, (2)-3-(6) µm x (1)-1-(2) µm; chlamydospores intercalary or terminal on lateral hyphae; uncommon; reported from soil, sporocarps of ectomycorrhizal fungi (Gams 1971); cellulolytic, gelatinolytic, utilizes starch.

Verticillium cephalosporium W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 180-181 (ALTA 10716).

From *S. fuscum* (D – 1). Conidia globose to subglobose, (2.0)-3.3-(4.3) µm x (1.0)-1.4-(1.8) µm; uncommon; reported from soil (Gams 1971); cellulolytic, gelatinolytic, utilizes starch.

Verticillium lecanii (Zimm.) Viégas, 1939, Revue Institute Café Sao Paolo 14: 754 (ALTA 10717).

From *C. aquatilis* rhizomes (D – 1) and leaves (D – 1), *S. fuscum* (D – 1). Conidia cylindrical to ellipsoidal, in slimy heads, (3.1)-4.7-(6.5) µm x (1.6)-1.9-(2.2) µm; cosmopolitan; reported from soil, insects, plant litter (see Domsch et al. 1980 for references); cellulolytic, chitinolytic (Domsch 1960), pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Verticillium psalliotae W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 184-186 (ALTA 10718).

From *S. fuscum* (L – 2, D – 10). Conidia sickle-shaped, apiculate, in slimy heads, (5.2)-6.7-(8.5) µm x (1.0)-1.2-(1.7) µm; widespread; reported from hypogeous and rust fungi, dung, soil, insects (see Domsch et al. 1980 for references); cellulolytic, gelatinolytic, utilizes starch.

CONCLUSIONS

Ninety-five species were obtained during the survey of fungi from the dominant vegetation of a bog and fen in southern boreal Alberta. These were three ascomycetes, ten basidiomycetes, 12 zygomycetes, and 70 fungi imperfecti. The majority of these species represent new records from the five substrates (*Sphagnum fuscum* plants, *Salix planifolia* leaves and roots, and *Carex aquatilis* leaves and rhizomes). There are undoubtedly many more fungi in these litters that alternative isolation techniques may have recovered. In addition, yeasts and *mycelia sterilia* were not included in this list, but were obtained during this survey.

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CHAPTER 4. THE MICROFUNGUS COMMUNITIES OF THE DECOMPOSING DOMINANT VEGETATION OF PEATLANDS IN SOUTHERN BOREAL ALBERTA, CANADA

INTRODUCTION

Peatlands cover approximately 4% of the world's landscape (National Wetlands Working Group 1988) and play a significant role in the global carbon cycle (Gorham 1991) by virtue of their significant peat deposits (approximately 50% carbon). The fungal communities (mycota) have been examined in a variety of peatlands in Antarctica (Baker 1970, Wynn-Williams 1980), Asia (Hiroki and Watanabe 1996), Australia (McLennan and Ducker 1954, Thrower 1954), Europe (Küster 1963, Latter et al. 1967, Dooley and Dickinson 1971, Dal Vesco 1974/75, Martin et al. 1982, Dawid 1984, Chmielewski 1991, Nilsson et al. 1992, Czeczuga 1993, Gilbert et al. 1998), and North America (Christensen and Whittingham 1965, Christensen and Cook 1970, Williams and Crawford 1983). These studies have investigated the mycota of hummocks and hollows of bogs, fens, swamps, moors, muskeg, and anthropogenically-altered wetlands.

A succession of fungi during the process of decomposition has been observed in a variety of plant species in terrestrial (Frankland 1966, Saitô 1966, Kasai et al. 1995, Lumley et al. 2001) and wetland (Pugh 1958, Pugh and Mulder 1971, Apinis et al. 1972, Cabral et al. 1993, Tokumasu 1994) ecosystems. Succession generally is defined as an orderly progression of changes, in which a pioneer community colonizes a particular substrate or ecosystems and, with time, culminates in a climax community. In contrast to succession in plant communities, terminating in a climax community, succession of saprophytic fungi results in the decomposition of the substrate and a climax community does not result. Fungal succession through time may be due to the process of facilitation, where species of a particular fungal community alter the substrate sufficiently to allow other species to become established and form a subsequent community (Lumley et al. 2001). For example, changes in litter quality, water potential of the litter, temperature, and pH have been shown to be important variables that determine the fungal community of a particular substrate (Pugh 1958, Christensen and Whittingham 1965, Pugh and Mulder 1971, Dix 1985, Nilsson et al. 1992, Lumley et al. 2001).

The objectives of this study were to evaluate the mycota of the dominant bog and fen vegetation (*Sphagnum fuscum* (Schimp.) Klinggr. from a bog and *Carex aquatilis* Wahlenb. leaves and rhizomes and *Salix planifolia* Pursh leaves and roots from a fen) in southern boreal

Alberta, Canada, and to determine the influence of environmental variables on these communities. These plant species were selected because of their significant contribution to the total net primary production (Szumigalski and Bayley 1997, Thormann and Bayley 1997) and accumulation of peat in peatlands of western continental Canada (Kuhry and Vitt 1996, Thormann et al. 1999a). I hypothesized that (1) the mycota of the dominant bog and fen plant species differ significantly and (2) distinct fungal successional patterns emerge during the decomposition of each of these litter types. Differences in the mycota and distinct successional patterns were expected because of different TC, TN, and TP tissue nutrient concentrations and TC:TN quotient of these plant tissues (Thormann et al. 2001) and significantly different pH and alkalinity-related variables and water levels between bogs and fens (Vitt 1994, Szumigalski and Bayley 1997, Thormann and Bayley 1997, Thormann et al. 2001).

METHODS

Study area and site descriptions

The riverine sedge fen (54° 28'N, 113° 18'W) and Perryvale bog (54° 28'N, 113° 16'W) lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). The area is characterized by mild summers and cold, snowy winters and a long-term mean annual temperature of 1.7 °C. The total mean annual precipitation is approximately 500 mm (Environment Canada 1982).

The fen is dominated by *Carex aquatilis*, *Carex lasiocarpa* Ehrh., *Salix planifolia*, and *Equisetum fluviatile* L. The bryophyte stratum is sparse and discontinuous and consists primarily of *Brachythecium mildeanum* (Schimp.) Schimp. *ex* Milde and *Tomenthypnum nitens* (Hedw.) Loeske. The bog is dominated by *Sphagnum fuscum*, *Sphagnum angustifolium* (C. Jens *ex* Russ.) C. Jens, *Picea mariana*, and members of the Ericaceae, including *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Andromeda polifolia* L. Vegetation composition, surface water chemistry, and physical parameters of both sites are provided in more detail elsewhere (Thormann et al. 1999b, Thormann et al. 2001, Chapters 2 and 6).

Sampling of living and decomposing plant material

In the bog, the top 3 cm of approximately 20 individual living, healthy-looking *Sphagnum fuscum* plants were collected in early May, July, and September 1997. In the fen, the top 10 cm of ten *Carex aquatilis* leaves, ten 10 cm segments of living *C. aquatilis* rhizomes, ten entire *Salix planifolia* leaves, and ten 10 cm terminal segments of *S. planifolia* roots were collected at the same time as the *S. fuscum* plants.

A two-year decomposition study using nylon mesh bags (3 x 6 cm, 1 mm gauge) was initiated in early September 1997 (Thormann et al. 2001, Chapter 2). Briefly, between five and eight individual fresh segments of each plant substrate were placed separately into each of 18 decomposition bags. Therefore, a total of 90 decomposition bags were deployed in the peatlands and placed horizontally approximately 2-5 cm below the peat surface (*Sphagnum fuscum* plants, *Carex aquatilis* rhizomes, and *Salix planifolia* roots) or on top of the peat surface (*S. planifolia* and *C. aquatilis* leaves) to mimic natural conditions of decomposition for these plant litters. Sets of triplicate decomposition bags were retrieved after 20 and 50 days in 1997, after eight and 12 months in May and September 1998, and after 20 and 24 months in May and September 1999. The living and decomposing plant tissues were then further processed to isolate microfungi from them.

Isolation and identification of filamentous microfungi

The living and decomposing plant material was cleaned by removing roots and other plant tissues using fine forceps and a dissecting microscope. Each of ten randomly selected, cleaned segments of each plant tissue was cut with a flame-sterilized scalpel into ten smaller segments. These were surface-sterilized for five minutes in 10% hydrogen peroxide (H_2O_2) and washed with sterilized, distilled water (d-H_2O) prior to placing them on three plates each of Potato Dextrose Agar (PDA, 39.0 g Difco potato dextrose agar, 1.0 L d-H_2O), PDA with rose bengal (0.03%), PDA with benomyl (0.0002%), and Mycobiotic agar® (MYC, containing cycloheximide, 35.6 g Difco mycobiotic agar, 1.0 L d-H_2O). All media were amended with oxytetracycline (0.01%) to suppress bacterial growth.

Plates were incubated at room temperature in the dark and fungi were sub-cultured onto Malt Extract Agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) as soon as they grew from the plant material. Plates were examined daily for emerging fungi for the first two weeks, weekly for the following six months, and monthly for the following two years of incubation. For identification purposes, slide cultures (Sigler 1993) on mixed cereal agar (Pablum®, H. J. Heinz Company of Canada Ltd., 100.0 g mixed cereal, 15.0 g Difco agar, 1.0 L d-H_2O) were prepared, mounted in polyvinyl alcohol, and examined on an Olympus BX50 compound microscope. Only fungi that produced distinctive diagnostic colony and morphological characters were enumerated in this investigation. Yeasts and sterile isolates represented less than 20% of all isolates and along with chytridiomycetes were excluded from this study.

Isolates were scored as separate records if they originated from different plant segments on the same primary isolation plate or if they originated from plant segments from different primary isolation plates. Multiple isolates from the same plant segment were scored as a single record. Representative living cultures and/or microscope slides have been deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH), the University of Alberta Cryptogamic Herbarium (ALTA), the Centraalbureau voor Schimmelcultures (CBS), and/or the Northern Forestry Centre (NoF) (Chapter 3, Appendix 4).

Statistical analyses

Canonical Correspondence Analyses (CCA) of each litter type (*Sphagnum fuscum*, *Carex aquatilis* leaves and rhizomes, and *Salix planifolia* leaves and roots) individually and in combination with each other were done using CANOCO (ter Braak 1992). This analysis ordinates communities and environmental variables, such that the relative position of the communities reflect their similarity/dissimilarity and the environmental variables are represented by vectors overlying the positions of the individual communities. The relative significance of the vectors is indicated by their length and direction from the axes origin.

Environmental variables included in the analyses were surface water chemistry (nitrate [NO_3^-], ammonium [NH_4^+], total dissolved nitrogen [TDN], soluble reactive phosphorus [SRP], total dissolved phosphorus [TDP], total phosphorus [TP], pH, conductivity, alkalinity, bicarbonate [HCO_3^-], dissolved organic carbon [DOC], calcium [Ca^{2+}], and potassium [K^+]), litter quality (total carbon [TC], total nitrogen [TN], total phosphorus [TP], and TC:TN quotients), and physical variables (peat temperature, water temperature, depth of the acrotelm). Pearson's correlation coefficients among all variables and the first and second CCA axes were generated from the ordinations. All ordination vectors were multiplied by 5 for a clearer representation in the figures.

RESULTS

I identified 95 fungal taxa (three ascomycetes, ten basidiomycetes, 12 zygomycetes, and 70 Fungi Imperfecti) from 883 filamentous microfungal records obtained during a survey of fungi from the dominant bog and fen plant species (*Sphagnum fuscum* from the bog, *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots from the riverine sedge fen).

The living and decomposing plant tissues of each of the five plant tissues had characteristic microfungal communities associated with them. Generally, ascomycetes and basidiomycetes were rarely isolated, and most were zygomycetes and Fungi Imperfecti (Table 4-1). Zygomycetes and Fungi Imperfecti dominated the fungal communities of living and decomposing *S. fuscum* (Table 4-1). Although ascomycetes and basidiomycetes were isolated more frequently from living *S. fuscum*, they were absent in the decomposing moss litter (Table 4-1). Conversely, ascomycetes and basidiomycetes were more dominant in decomposing than living *C. aquatilis* leaves (Table 4-1). Isolation frequencies of all fungal species from each litter type are listed in Table 4-2.

Isolation frequencies of the five most common fungal taxa of each decomposing litter type ranged from 4 to 45% (*Penicillium funiculosum* and *Phialophora cf. alba* from *C. aquatilis* rhizomes, respectively) (Figure 4-1). *Phialophora cf. alba* was the most common fungus isolated from *C. aquatilis* rhizomes (45%), where its frequency exceeded that of the next four most common taxa in this litter type together (Figure 4-1). Species of *Trichoderma* were common in all five litter types and represented between 4 and 7% of all isolates. Similarly, *Mucor hiemalis* was one of the five most common species in four of the five litter types and represented between 7 and 17% of all isolates (Figure 4-1). The remaining fungal taxa were isolated less frequently.

Fungal community analyses

The mycota of decomposing *Sphagnum fuscum* plants, *Carex aquatilis* rhizomes, and *Salix planifolia* roots were significantly different from each other and formed distinct clusters. However, the mycota of decomposing *C. aquatilis* and *S. planifolia* leaves were indistinct and similar to each other (Figure 4-2A). CCA revealed that the mycota of *S. fuscum* showed a strong correlation with the TC:TN quotient of the litter, while the fen litter mycota were more influenced by TC, TN, and TP tissue nutrient concentrations (Figure 4-2A, Table 4-3). Eigenvalues for axes 1 and 2 were 0.568 and 0.392, respectively. Fungi involved in the decomposition of the bog and fen plant litters separated along axis 1 and generally formed distinct communities (Figure 4-2B). Several species of *Mortierella* and *Verticillium* occurred almost exclusively in the bog, while species of *Phialophora*, *Phialocephala*, and basidiomycetes were isolated almost exclusively from the fen vegetation. Species of *Trichoderma*, *Acremonium*, and *Mucor* occurred in both fen and bog litters (Figure 4-2B, Table 4-2).

The mycota of decomposing *Sphagnum fuscum* in the bog separated along axis 1 (Figure 4-3A). Fungal taxa isolated during the initial stages of decomposition (0-20 days) strongly correlated with TP surface water concentrations, while those involved with the later stages of decomposition (1-2 years) were strongly correlated with pH and tissue nutrient concentrations of TP and TC (Figure 4-3A, Table 4-4). Eigenvalues for the first and second axis were 0.367 and 0.255, respectively. Environmental variables were unable to explain the distribution of individual fungal genera isolated from the decomposing bryophyte litter (Figure 4-3B). For example, species of *Penicillium* and *Mortierella* did not cluster together but were common throughout all stages of decomposition (Figure 4-3B, Table 4-2).

Distinct fungal communities were involved in the decomposition of above and belowground litters of *Carex aquatilis* (leaves and rhizomes) in the fen (Figure 4-4A). Separation of the mycota along axis 1 indicated a clear succession of fungi of the decomposing *C. aquatilis* leaves, with early stage decomposition communities on the left side and late stage decomposition communities on the right side of axis 1. There were no trends in fungal succession of the *C. aquatilis* rhizome litter (Figure 4-4A). The mycota of the leaf litter correlated with TP and TN tissue nutrient concentrations, at least during the later stages of decomposition. The mycota of the sedge rhizomes generally showed a strong correlation to the TC:TN quotient (Figure 4-4A, Table 4-5). Eigenvalues for axes 1 and 2 were 0.619 and 0.597, respectively. Axis 2 separated the fungi isolated from the decomposing above and belowground litters, with those species isolated from both litters found between them (Figure 4-4B). Species of *Cladosporium* and basidiomycetes occurred almost exclusively in the leaf litter, while species of *Phialophora* and *Phialocephala* were isolated almost exclusively from the rhizome litter. Species of *Penicillium* and *Mucor* occurred in both *C. aquatilis* leaf and rhizome plant tissues (Figure 4-4B, Table 4-2).

Similarly, the mycota involved in the decomposition of the belowground litters in the fen (*Carex aquatilis* rhizomes and *Salix planifolia* roots) separate along axis 1 (Figure 4-5A). Although a weak successional pattern of the microfungi of *C. aquatilis* rhizomes was apparent along axis 2, no discernible pattern was apparent for *S. planifolia* roots (Figure 4-5A). TC and TN tissue nutrient concentrations correlated with the mycota of the roots, whereas TP tissue nutrient concentrations and the TC:TN quotient correlated with the mycota of the rhizomes (Figure 4-5A, Table 4-6). Eigenvalues for axes 1 and 2 were 0.568 and 0.385, respectively. Although the mycotas separated well along Axis 1, few microfungi were restricted to either of the two belowground litters and most of the fungal taxa were shared between them (Figure 4-5B). For example, several unidentified pycnidial taxa and some species of *Penicillium* occurred almost exclusively in the *C. aquatilis* rhizome litter, while species of *Verticillium* and

Monocillium were isolated almost exclusively from the *S. planifolia* root litter. Species of *Trichoderma*, *Phialophora*, and *Phialocephala* occurred in the *C. aquatilis* rhizome and *S. planifolia* root litters alike (Figure 4-5B, Table 4-2). None of the other litter type by litter type comparisons showed significant trends in their mycota and no successional patterns were apparent in those data (data not shown).

DISCUSSION

Differences in the mycota involved in the decomposition of the dominant fen and bog vegetation

There were distinct differences in the mycota of decomposing bog and fen vegetation (Figure 4-2A). The mycota associated with decomposing *Sphagnum fuscum* in the bog formed a very distinct, tight cluster, while the mycota associated with decomposing *Carex aquatilis* rhizomes and *Salix planifolia* roots formed less confined clusters (Figure 4-2A). The mycota of the decomposing sedge and willow leaves did not form well-defined clusters and were dispersed throughout the mycotas of the belowground litters (Figure 4-2A). These data indicate that distinct fungal communities were associated with plant litters in close contact with the soil in each site, whereas the mycota associated with litters of an aerial origin were less specific.

Several studies have investigated the mycota of peatlands in the past (Christensen and Whittingham 1965, Latter et al. 1967, Dooley and Dickinson 1971, Nilsson et al. 1992); however, none of these studies investigated the mycota specifically associated with plants whose remains constitute the bulk of the accumulated peat. Furthermore, Christensen and Cook (1970), Williams and Crawford (1983), and Hiroki and Watanabe (1996) examined physiological traits of microbial communities (bacteria and fungi) in peat. All of these studies indicated different fungal assemblages among different peatlands, at different depths within the peat, between hummocks and hollows within the same peatland, and between natural and anthropogenically altered peatlands. Furthermore, the mycota of peatland plant species throughout the process of decomposition has rarely been investigated. Christensen and Cook (1970) and Nilsson et al. (1992) examined the mycota of peat at different depths, a proxy for different stages of the decomposition process of peat; however, the age and degree of decomposition of their peat samples were not determined in their studies.

Dooley and Dickinson (1971) recognized two distinct fungal communities in peat: a cosmopolitan community and an indigenous community. Their cosmopolitan community consisted of species common to soils around the world, such as *Aspergillus fumigatus*, *Penicillium* spp., *Trichoderma viride*, and *Mortierella elongata*. In contrast, *Oidiodendron* *griseum*, *Phialophora* sp., and *Torulomyces lagena* Delitsch were some of their indigenous fungi, restricted to specific soil types. Their community classes (indigenous *vs*. cosmopolitan) also can be applied to the fungi isolated in this study. Of the 95 fungi identified, 25 species were isolated exclusively from the bog litter (26%), while 49 species (52%) were isolated only from the decomposing fen litters. Twenty-one species (22%) were common to the fen and bog litters. Some of the species restricted to decomposing *Sphagnum fuscum* were species of *Aspergillus* (*A. niger*, *Aspergillus versicolor*), *Mortierella* (*M. horticola*, *M. humilis*, *M. ramanniana*), *Verticillium* (*V. bulbillosum*, *V. cephalosporium*, *V. psalliotae*), and *Oidiodendron* (*O. maius*, *O. scytaloides*) (Figure 4-2B, Table 4-2). Species restricted to the decomposing fen litters were species of *Phialophora* (*P. alba*, *P. cf. alba*), *Phialocephala* (*P. dimorphospora*, *P. fortinii*), *Fusarium* (*F. oxysporum*, *F. sporotrichioides*), and several unidentified basidiomycetes (Figure 4-2B). These would represent the indigenous mycota of these two peatlands, according to Dooley and Dickinson (1971). The cosmopolitan community consisted largely of species of *Mortierella* (*M. elongata*, *M. isabellina*), *Trichoderma* (*T. viride*, *T. harzianum*), and *Mucor hiemalis* (Figure 4-2B). Although the species of the cosmopolitan and indigenous fungal communities vary between Dooley and Dickinson's (1971) and this study, these differences can be ascribed to environmental and site differences. Furthermore, I only examined the mycota of one litter type in the bog. An investigation of additional litter types in this site would likely reveal microfungi also shared with the fen litters.

The occurrence of specific fungi in peatlands *vs*. other ecosystems has been ascribed most often to pH, water-logging, and temperature (Christensen and Whittingham 1965, Latter et al. 1967, Nilsson et al. 1992). None of these environmental variables accounted for the variation of the mycota of these five decomposing peatland plant litters (Figure 4-2A). Instead, litter quality variables, such as TN, TP, and TC:TN, significantly correlated with axes 1 and 2 (Table 4-3) and separated the mycota of most of the litter types, results similar to those of Pugh and Mulder (1971), who determined that the distribution of some fungi in their *Typha latifolia* L. litter was affected by the nutrient status of the litter at various stages of decomposition. Here, the mycota of *Sphagnum fuscum* and *Carex aquatilis* rhizomes were correlated with a high TC:TN quotient. These two litter types had the highest TC:TN quotients (45-73) of the five litters (Thormann et al. 2001). In contrast, the mycota of the *Salix planifolia* litter types (leaves and roots) seemed to be adapted to higher tissue concentrations of TC (Figure 4-2A). These litters had the highest TC tissue concentrations of the five litters (Thormann et al. 2001). Therefore, the mycota of these five litter types were primarily influenced by litter quality variables and not by external variables, despite significant differences in several surface water chemistry and physical variables between the bog and fen (Thormann et al. 2001).

Succession of the mycota of decomposing peatland vegetation

The mycota of *Sphagnum fuscum*

The CCA of the mycota of decomposing *Sphagnum fuscum* shows a clear pattern of succession, with axis 1 separating the early and late stage fungal communities (Figure 4-3A). The mycota of the early stages of decomposition of this bryophyte were related to elevated TP surface water concentrations and lower tissue nutrient concentrations of TC and TP (Figure 4-3A, Table 4-4). Species of *Aspergillus* (*A. niger*, *A. versicolor*) and *Trichoderma* (*T. harzianum*, *T. polysporum*) were among those isolated exclusively from early-stage decomposing *S. fuscum* (Table 4-2). Conversely, *Oidiodendron scytaloides*, the *Sporothrix* state of *Ophiostoma stenoceras*, *Mortierella isabellina*, and several species of *Acremonium* (*A. cf. curvulum*, *A. chrysogenum*, *A. strictum*) appeared only in well-decomposed *S. fuscum* (Table 4-2). These species were affected by elevated tissue nutrient concentrations of TC and TP and higher acidity of the surface water (Figure 4-3B). Several fungal species were not affected by changes in litter quality, environmental variables, and surface water chemistry. For example, most species of *Mortierella*, *Penicillium*, *Trichoderma*, and *Mucor hiemalis* occurred throughout the entire decomposition period (Table 4-2).

Despite site and environmental variation, Christensen and Whittingham (1965), Latter et al. (1967), Dooley and Dickinson (1971), and Nilsson et al. (1992) previously investigated the mycota of peat. Their mycota is remarkably similar to mine, with species of *Trichoderma*, *Mortierella*, *Verticillium*, and *Penicillium* constituting a major proportion of the taxa. Although water levels, pH, temperature, and the vegetation composition of peatlands influence the relative abundance of different fungal species (Whittingham 1965, Latter et al. 1967, Dooley and Dickinson 1971, Nilsson et al. 1992), the fungal species richness generally appears to be similar among peatlands.

Of those fungi isolated from peat, few have been examined for their ability to decompose species of *Sphagnum*. Tsuneda et al. (2001) examined the decomposition process of *Sphagnum fuscum* by *Oidiodendron maius* and *Acremonium cf. curvulum* and found them to have different methods of cell wall degradation of the leaf tissues. I examined mass losses of *S. fuscum* caused by nine fungi isolated from living and decomposing *S. fuscum* (Appendix 3). My mass losses ranged from 0.5-10.2% after eight weeks and are considerably lower than those reported by Czastukhin (1967) (13-22% after one year).

The mycota of *Carex aquatilis* leaves and rhizomes

Comparison of their mycotas

The CCA of the mycota of decomposing *Carex aquatilis* leaves and rhizomes shows a clear separation of the mycota of these two litter types along axis 2, with the mycota of the decomposing rhizomes and leaves being clustered above and below axis 1, respectively (Figure 4-4A). TP and TN tissue nutrient concentrations and the TC:TN quotient of the decomposing sedge litters correlate with the mycota of these litters (Figure 4-4A), correlating significantly with axis 2 (Table 4-5).

Of all fungi isolated from decomposing *Carex aquatilis* leaves, 52% occurred exclusively in the leaves, with the remainder being found in both leaves and rhizomes. Similarly, 47% of the fungi isolated from its rhizomes occurred exclusively in the rhizomes (Table 4-2). Species of *Cladosporium* (*C. cladosporioides*, *C. herbarum*), *Monocillium* (*M. constrictum*, *M. nordinii*), and all unidentified basidiomycetes (spp. 2, 3, 4, 5, 7, and 8) were isolated only from decomposing sedge leaves. Conversely, species of *Fusarium* (*F. aquaeductuum* var. *medium*, *F. oxysporum*), *Trichoderma* (*T. aureoviride*, *T. piluliferum*, *T. pseudokoningii*), and several unidentified pycnidial species (sp. 1, 2, and 5) occurred only on the decomposing sedge rhizomes. Species of *Phialophora* (*P. alba*, *P. cf. alba*), *Trichoderma* (*T. harzianum*, *T. viride*, *T. koningii*), and *Penicillium* (*P. chrysogenum*, *P. funiculosum*, *P. purpurogenum*, *P. thomii*) were common to both sedge litters (Table 4-2).

Carex aquatilis leaves

A clear succession pattern was apparent for the mycota of decomposing *Carex aquatilis* leaves, with axis 1 separating the mycota of different decomposition stages (Figure 4-4A). The mycota of the early stages of decomposition (0-50 days) occurred on the left side of axis 1 and those of the late stages of decomposition (250-730 days) occurred on the right side of axis 1 (Figure 4-4A). Early-stage successional species primarily belonged to *Cladosporium*, *Botrytis*, and *Acremonium*, while those of the later stages of decomposition primarily belonged to *Monocillium* and *Dimorphospora* as well as some of the unidentified basidiomycetes (Figure 4-4A, Table 4-2).

Although studies on the mycota of wetland plant species, such as species of *Juncus*, *Phragmites*, and *Typha*, are not uncommon (Latter and Cragg 1967, Pugh and Mulder 1971, Apinis et al. 1972, Fell and Hunter 1979, Cabral et al. 1993, Tokumasu 1994), those investigating the mycota of species of *Carex* are rare (Pugh 1958). What is remarkable is the occurrence of similar fungal genera on the living and decomposing leaves of different plant species. Species of *Cladosporium*, *Fusarium*, *Alternaria*, *Trichoderma*, *Penicillium*, *Mortierella*, *Acremonium*, and *Epicoccum* occur equally frequently and constitute some of the primary colonizers and saprophytes of aerial plant tissues. General succession patterns of those studies indicate that species of *Alternaria*, *Aureobasidium*, *Cladosporium*, *Epicoccum*, and *Fusarium* occur during early stages of decomposition, while species of *Mucor*, *Oidiodendron*, *Penicillium*, and *Phoma* occur during later stages of decomposition (Latter and Cragg 1967, Apinis et al. 1972). Those patterns are supported by this study, as isolation frequencies of species of the above genera follow similar trends in decomposing *Carex aquatilis* leaves in this fen (Table 4-2).

Carex aquatilis rhizomes

In contrast, a clear fungal succession pattern was absent for the mycota of decomposing *Carex aquatilis* rhizomes (Figure 4-4), possibly a reflection of the low number of identified species from this substrate (Table 4-2). However, several species of *Trichoderma* were only isolated during later stages of decomposition. Similarly, although species of *Phialophora* and *Phialocephala* were isolated from most stages of decomposition, their isolation frequencies increased with increasing decomposition (Table 4-2).

Very few studies have examined the mycota of belowground litters of wetland plant species. Pugh and Mulder (1971) examined the mycota of *Typha latifolia* rhizomes and roots. Their rhizomes were almost mycologically sterile, with only few dematiaceous, sterile taxa present. Their roots also showed a limited range of fungal richness (*Aureobasidium pullulans*, *Cladosporium herbarum*, *Helicorhoidion* sp., *Isaria* sp., and one *mycelium sterilium*) (Pugh and Mulder 1971). Similarly, I identified the lowest number of fungi from decomposing *Carex aquatilis* rhizomes (Table 4-2), possibly a reflection of the decreasing isolation frequency of fungi with increasing depth within a soil column due to oxygen limitations. The mean oxygenated peat horizon (acrotelm) depth was 6 cm below the peat surface (Thormann et al. 2001) and the decomposition bags with the belowground fen litters were buried between 2-5 cm below the peat surface to mimic natural decomposition conditions. Therefore, the rhizome litter may have been exposed to low oxygen concentrations for part of the two-year decomposition period, thereby limiting fungal species richness.

The mycota of *Carex aquatilis* rhizomes and *Salix planifolia* roots

Comparison of their mycotas

The mycota decomposing belowground litters of the sedge and willow in the fen differed substantially (Figure 4-5A). The mycota of the decomposing *Salix planifolia* roots showed a strong correlation to TN and TC tissue nutrient concentrations. These two litter quality variables significantly correlated with axes 1 and 2, respectively (Table 4-6). In contrast, the mycota of decomposing *Carex aquatilis* rhizomes primarily were affected by TP tissue nutrient concentrations and the TC:TN quotient (Figure 4-5A), with these litter quality variables being significantly correlated with axes 2 and 1, respectively (Table 4-6).

Thirty-seven percent of all species isolated from the rhizome litter occurred exclusively in the rhizomes, while 49% of all fungi isolated from the root litter occurred exclusively on the root litter. Species of *Penicillium* (*P. chrysogenum*, *P. funiculosum*), *Phialocephala* (*P. dimorphospora*, *P. fortinii*), *Phialophora* (*P. alba*, *P. cf. alba*), and *Trichoderma* (seven species) occurred on both litters (Figure 4-5B, Table 4-2). Conversely, species of basidiomycetes (*Armillaria sinapina*, *Bjerkandera adusta*) and several unidentified pycnidial species (spp. 1, 2, 5) occurred only on decomposing *Carex aquatilis* rhizomes and leaves. Species of *Mortierella* (*M. alpina*, *M. ericetorum*), *Monocillium* (*M. constrictum*, *M. nordinii*), and several unidentified pycnidial species (spp. 3, 6, 7) were isolated exclusively from decomposing *Salix planifolia* roots (Figure 4-5B, Table 4-2).

Salix planifolia roots

Species of *Acremonium*, *Cladosporium*, and *Fusarium* occurred primarily in early-stage decomposing *Salix planifolia* roots, while species of *Phialophora* and *Phialocephala* were more frequently isolated from the mid- and late-stage decomposing root material (Table 4-2). Studies investigating fungi associated with roots of woody plant species usually concentrate on mycorrhizal fungi, while the saprophytic mycota is less commonly investigated (Harley and Waid 1955, Livingston and Blaschke 1984, Summerbell 1989). Summerbell (1989) isolated primarily *mycelia sterilia*, some belonging to the *Mycelium radicis atrovirens* (MRA) complex (*sensu* Melin 1923), and species of *Mortierella* and *Penicillium* from *Picea mariana* roots and concluded that his rhizosphere fungi were not restricted to mycorrhizal roots of black spruce, but overlap considerably with those of other plant species. I isolated two MRA species as well (*Phialocephala dimorphospora* and *Phialocephala fortinii*), both of which were isolated at higher frequencies from mid- and late-stage decomposing *Salix planifolia* roots (Table 4-2). Overall, genera of microfungi isolated by Summerbell (1989) are similar to those isolated in this study, with several species of *Mortierella*, *Penicillium*, and *Trichoderma* frequently isolated from both substrata (Table 4-2).

Similar isolation frequency patterns were described above for decomposing *Carex aquatilis* rhizomes. It is likely that the environmental, physical, and surface water chemical variables measured, the similarity of the mycota of these two litter types, the relatively low number of identified species of either litter, and cultural techniques were not sufficient to show a clear succession pattern of some of these litter types throughout the process of decomposition.

CONCLUSIONS

An investigation into the mycota of decomposing vegetation from two southern boreal peatlands in Alberta, Canada, revealed substantially different fungal communities among different plant litters. A CCA showed a clear separation of the mycota of the dominant bog (*Sphagnum fuscum* plants) and fen (*Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots) plant species, supporting hypothesis one. Distinct succession patterns of the mycota of two of the five litter types were observed (*Sphagnum fuscum*, *C. aquatilis* leaves), with the remaining three litter types showing no clear succession patterns, thereby rejecting hypothesis 2. Litter quality variables (TC, TN, and TP tissue concentrations and TC:TN quotients) correlated most often with the observed fungal communities of these litter types, indicating that these variables were more important to the individual fungal communities than either physical or surface water chemistry variables measured in these two peatlands.

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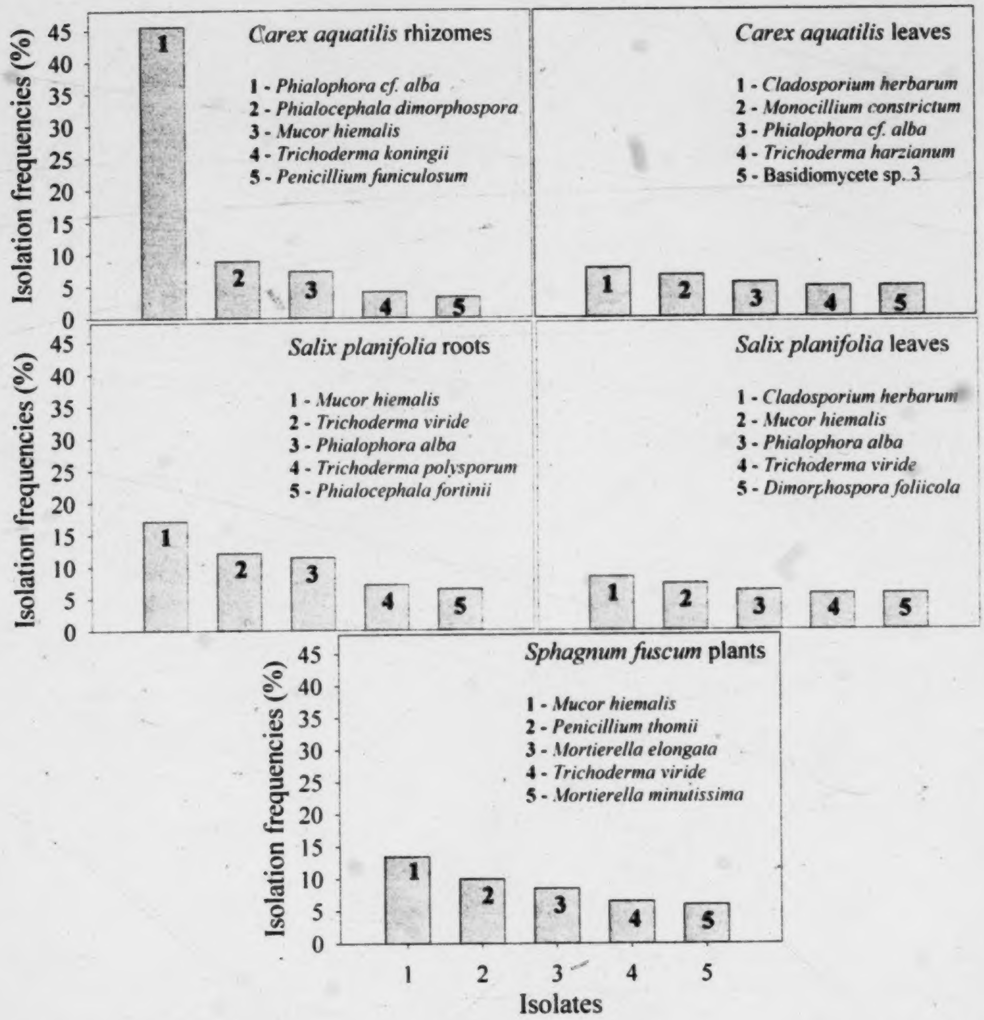

Figure 4-1. Isolation frequencies of the five most commonly isolated filamentous microfungi of decomposing *Sphagnum fuscum* plants from the Perryvale bog and *Salix planifolia* leaves and roots and *Carex aquatilis* leaves and rhizomes from the riverine sedge fen in southern boreal Alberta, Canada.

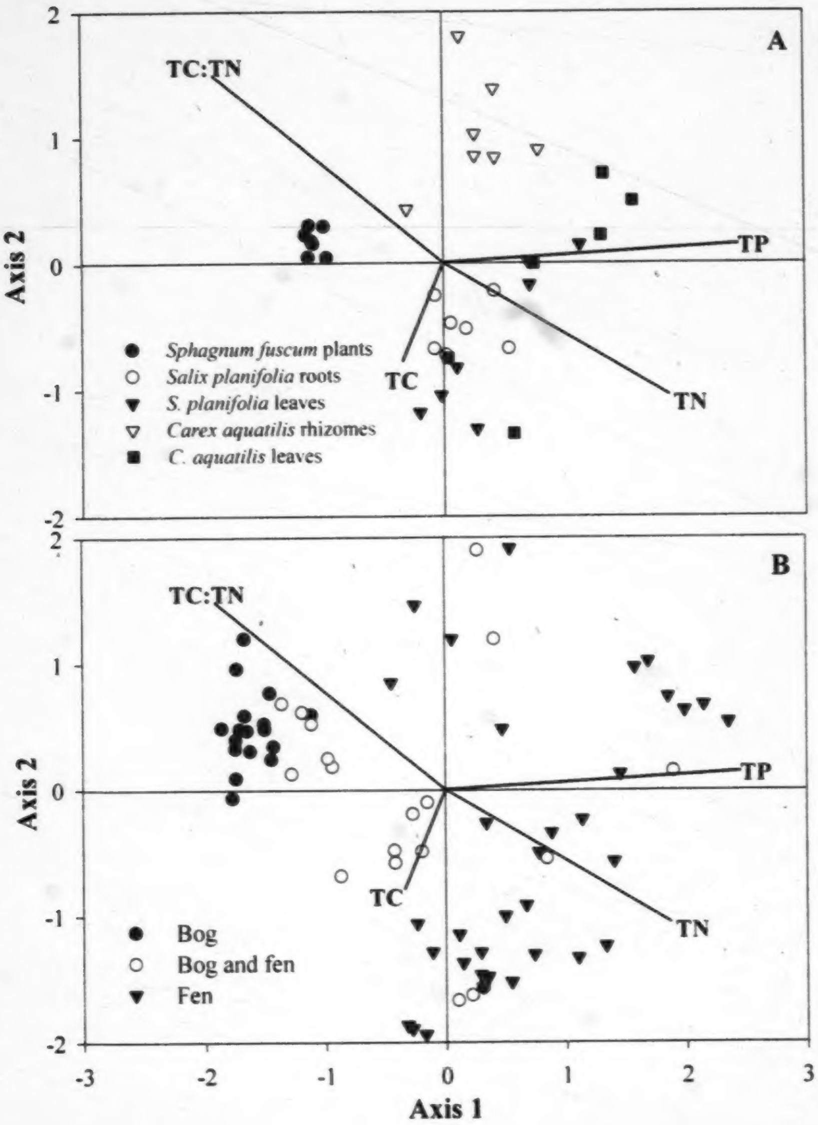

Figure 4-2. Canonical correspondence analyses of microfungus communities isolated at various stages of decomposition over a two-year period from two peatlands in southern boreal Alberta, Canada. **A** - Fungal communities from *Sphagnum fuscum* plants from the Perryvale bog, and *Salix planifolia* leaves and roots and *Carex aquatilis* leaves and rhizomes from the riverine sedge fen. **B** - Fungal species isolated from bog and fen litters. TC = total carbon, TN = total nitrogen, TP = total phosphorus.

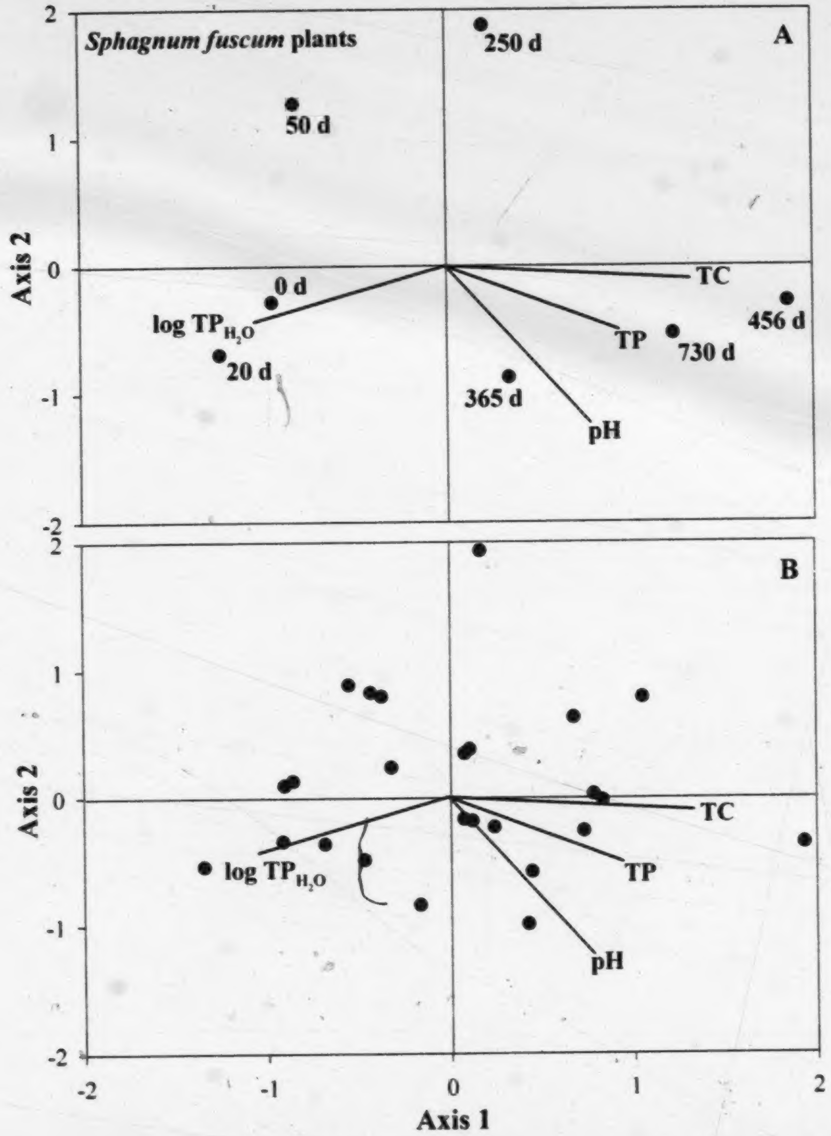

Figure 4-3. Canonical correspondence analyses of microfungus communities isolated at various stages of decomposition over a two-year period from the Perryvale bog in southern boreal Alberta, Canada. **A** - Fungal communities from *Sphagnum fuscum* plants. **B** - Fungal species isolated from *S. fuscum* plants. Abbreviations as in Figure 4-2, TP$_{H2O}$ = surface water concentration of total phosphorus.

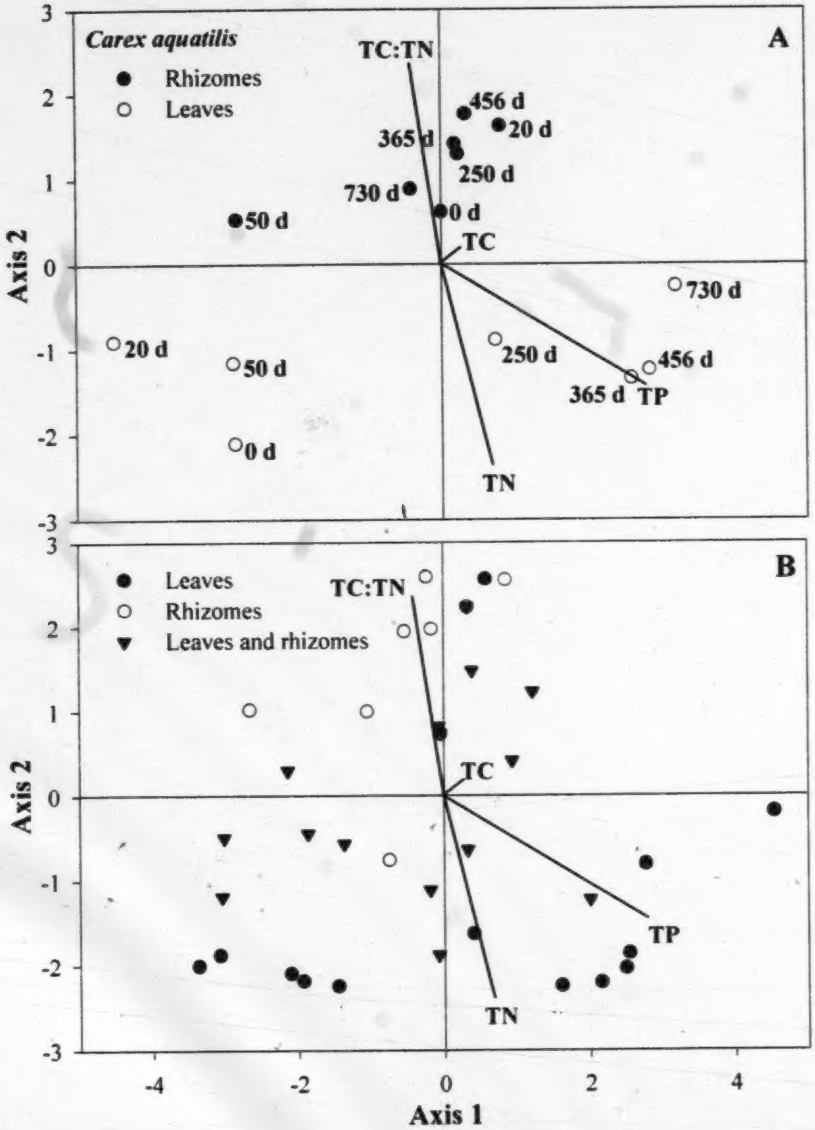

Figure 4-4. Canonical correspondence analyses of microfungus communities isolated a various stages of decomposition over a two-year period from the riverine segde fen in southern boreal Alberta, Canada. **A** - Fungal communities from *Carex aquatilis* leaves and rhizomes. **B** - fungal species isolated from *C. aquatilis* leaves and rhizomes. Abbreviations as in Figure 4-2.

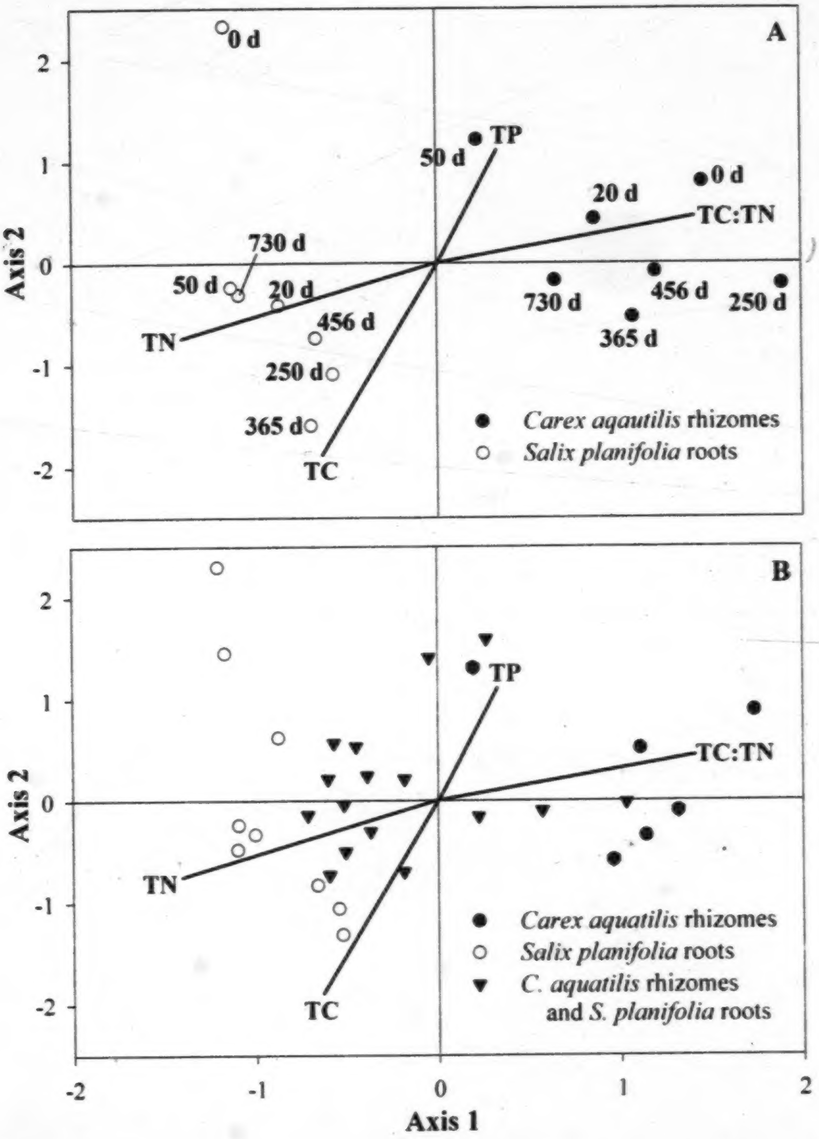

Figure 4-5. Canonical correspondence analyses of microfungus communities isolated at various stages of decomposition over a two-year period from the riverine sedge fen in southern boreal Alberta, Canada. **A** - Fungal communites from *Salix planifolia* roots and *Carex aquatilis* rhizomes. **B** - Fungal species isolated from *S. planifolia* roots and *C. aquatilis* rhizomes. Abbreviations as in Figure 4-2.

Table 4-1. Isolation frequencies of ascomycetes (A), basidiomycetes (B), zygomycetes (Z), and Fungi Imperfecti (FI) from living and decomposing plant material from two peatlands in southern boreal Alberta, Canada.

Sites	Litter types		Isolation frequencies (%)			
			A	B	Z	FI
Bog	*Sphagnum fuscum* plants	Living	8.0	5.7	40.9	45.4
		Decomposing	0.6	0.0	45.6	52.8
		Mean	3.1	1.9	44.7	50.3
RSF	*Carex aquatilis* leaves	Living	0.0	0.0	5.2	94.8
		Decomposing	17.9	18.9	8.5	54.7
		Mean	11.6	12.2	7.3	68.9
	C. aquatilis rhizomes	Living	0.0	4.2	0.0	95.8
		Decomposing	0.0	0.9	10.7	88.4
		Mean	0.0	1.5	8.8	89.7
	Salix planifolia leaves	Living	0.0	4.3	4.3	91.4
		Decomposing	0.9	6.3	15.2	77.6
		Mean	0.6	5.7	12.0	81.6
	S. planifolia roots	Living	0.0	0.0	19.1	80.9
		Decomposing	0.0	0.0	23.3	76.7
		Mean	0.0	0.0	22.1	77.9

Note: RSF = riverine sedge fen.

Table 4-2. Isolation frequencies (%) of fungi from decomposing *Sphagnum fuscum* plants from a bog and *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots from a fen in southern boreal Alberta, Canada.

Substrates	Fungi	Decomposition period (days)						
		0	20	50	250	365	456	730
S. fuscum plants	*Acemonium cf. curvulum* W. Gams		0.50			1.00		
	Acremonium chrysogenum (Thisum. & Sukop.) W. Gams					0.50		
	Acremonium strictum W. Gams					0.50		
	Aspergillus niger van Tieghem		0.50					
	Aspergillus versicolor (Vuill.) Tiraboschi		0.50					
	Botrytis cinerea Pers. *ex* Pers.		0.50					
	Cladosporium herbarum (Pers.) Link *ex* Gray	0.50						
	Kernia retardata Udagawa & Muroi					0.50		
	Mortierella alpina Peyronel		0.50			1.00		
	Mortierella elongata Linnem.	2.50	3.00	1.00		1.50		0.50
	Mortierella horticola Linnem.	0.50	1.00		0.50			
	Mortierella humilis Linnem.	0.50						
	Mortierella isabellina Oudem. & Koning				1.00	1.50	1.00	
	Mortierella minutissima van Tieghem	1.00	0.50	1.00	0.50	2.00	1.00	
	Mortierella ramanniana var. *angulispora* (Möller) Linnem.	1.50	0.50			2.00	2.00	
	Mortierella ramanniana var. *ramanniana* (Naumov) Linnem.	0.50		0.50	1.00	1.00		0.50
	Mortierella renispora Dixon-Stewart	0.50	1.00			0.50		0.50
	Mortierella verticillata Linnem.	0.50			0.50			
	Mucor hiemalis Wehmer	0.50	2.50	2.00	4.00	2.00	2.50	
	Mycelium sterilium 4				0.50			

	Mycelium sterilium 5							0.50
	Mycelium sterilium 6				1.00			
	Mycelium sterilium 8						0.50	
	Mycelium sterilium 9						0.50	
	Mycelium sterilium 10						1.00	
	Nodulisporium sp.						0.50	
	Oididendron maius Barron			0.50				
	Oidiodendron scytaloides Gams & Söderström							0.50
	Penicillium funiculosum Thom	1.00		1.00	1.00			
	Penicillium montanense Christensen & Backus				0.50		0.50	
	Penicillium odoratum Christensen & Backus				1.00	0.50	0.50	
	Penicillium purpurogenum Stoll	0.50						
	Penicillium thomii Maire	0.50	2.50	0.50	1.50	3.00	1.50	0.50
	Sporothrix sp. 1					0.50		1.50
	Sporothrix state of *Ophiostoma stenoceras* (Robak) Melin & Nannf.							1.50
	Trichoderma aureoviride Rifai							1.00
	Trichoderma harzianum Rifai		1.00					
	Trichoderma polysporum (Link *ex* Pers.) Rifai			1.00				
	Trichoderma viride Pers. *ex* Gray	0.50	0.50		1.00	3.00		1.50
	Verticillium bulbillosum W. Gams & Malla	1.00	2.00	1.00	0.50			
	Verticillium cephalosporium W. Gams				0.50			
	Verticillium lecanii (Zimm.) Viégas			0.50				
	Verticillium psalliotae W. Gams	1.00	1.00	1.00	1.50	1.50		
C. aquatilis leaves	*Acremonium butyri* (van Beyma) W. Gams							0.53
	Acremonium strictum		0.53	0.53				
	Acremonium state of *Nectria rishbethii* Booth			0.53				
	Armillaria sinapina Bérubé & Dessur.		0.59				0.59	
	Aureobasidium pullulans var. *melanogenum* (de Bary) Arn.	1.78						

Basidiomycete sp. 2		0.59					
Basidiomycete sp. 3					0.59	3.56	0.59
Basidiomycete sp. 4					1.78		2.37
Basidiomycete sp. 5			0.59				
Basidiomycete sp. 7		0.59					
Basidiomycete sp. 8			0.59				
Botrytis cinerea	1.78	1.19					
Cladosporium cladosporioides (Fres.) de Vries	0.59						
Cladosporium herbarum	3.56		1.19				
Dimporphospora foliicola Tubaki				0.59		3.56	
Epicoccum purpurascens Ehrenb. *ex* Schlecht.	0.59						
Monocillium constrictum W. Gams				0.59		6.53	0.59
Monocillium nordinii (Bourchier) W. Gams				0.59		1.19	
Mortierella elongata		1.19	0.59				
Mortierella minutissima			0.59				
Mucor hiemalis		1.19	1.78				
Nodulisporium sp.					1.78		
Penicillium chrysogenum Thom						2.37	
Penicillium funiculosum			2.37				
Penicillium odoratum					0.59		
Penicillium thomii				0.59			
Phialophora alba		0.59		2.37		0.59	0.59
Phialophora cf. alba				1.19		3.56	1.78
Stagonospora caricis (Oud.) Sacc.	1.19						
Trichoderma harzianum		1.19		2.37		1.78	
Trichoderma koningii Oud.						1.19	
Trichoderma viride		0.59		0.59			
Verticillium lecanii							0.59

C. aquatilis rhizomes	*Acremonium strictum*		0.81					
	Armillaria sinapina	0.81						
	Arthrinium state of *Apiospora montagnei* Sacc.					0.81		
	Bjerkandera adusta (Willd.: Fr.) Karst.				0.81			
	Fusarium aquaeductuum var. *medium* Wollenw.	0.81						
	Fusarium oxysporum Schlecht.	0.81						
	Mortierella elongata			0.81				
	Mortierella isabellina				0.81			
	Mortierella minutissima			0.81				
	Mucor hiemalis			4.07		0.81	1.63	0.81
	Penicillium chrysogenum					0.81		
	Penicillium funiculosum			3.25				
	Penicillium purpurogenum	0.81						
	Penicillium thomii				0.81	0.81		
	Phialocephala dimorphospora Kendrick	0.81		2.44	1.63	0.81	3.25	
	Phialocephala fortinii Wang & Wilcox	0.81				1.63		
	Phialophora alba van Beyma	1.63					1.63	
	Phialophora cf. alba	2.44	7.32	2.44	4.88	4.88	15.4	8.13
	Pycnidial sp. 1			0.81				
	Pycnidial sp. 2				2.44			
	Pycnidial sp. 5			0.81				
	Scopulariopsis brevicaulis		0.81					
	Trichoderma aureoviride		0.81					
	Trichoderma harzianum							0.81
	Trichoderma koningii		2.44				1.63	
	Trichoderma piluliferum Webster & Rifai							0.81
	Trichoderma polysporum		2.44			0.81		
	Trichoderma pseudokoningii Rifai							1.63
	Trichoderma viride							1.63

	Verticillium lecanii			0.81				
S. planifolia leaves	*Acremonium* state of *Nectria rishbethii*	0.56						
	Alternaria alternata (Fr.) Keissler	2.78	1.11	1.11				
	Armillaria sinapina						0.56	1.67
	Arthrinium state of *Apiospora montagnei*		1.11	0.56				
	Aureobasidium pullulans var. *melanogenum*	1.67						
	Aureobasidium pullulans var. *pullulans* (de Bary) Arn.	0.56						
	Basidiomycete sp. 4					1.11		
	Basidiomycete sp. 6				0.56			
	Botrytis cinerea	0.56	1.11	0.56				
	Cladosporium cladosporioides	1.11	0.56					
	Cladosporium herbarum	2.78	1.11	1.67	2.78			
	Dimorphospora foliicola					1.67	3.34	0.56
	Fusarium chlamydosporum Wollenw. & Reink.		0.56					
	Mortierella elongata						1.67	
	Mortierella isabellina			0.56				
	Mucor hiemalis	1.11	1.11	0.56	2.78		0.56	1.11
	Nodulisporium sp.					1.11		
	Penicillium funiculosum			1.11				
	Phialocephala dimorphospora				0.56			
	Phialophora alba	0.56			1.11	0.56	1.11	2.78
	Phialophora cf. alba					1.11		1.11
	Polyscytalum cf. hareae		0.56	1.11	0.56			
	Scopulariopsis brevicaulis (Sacc.) Bain.		0.56					
	Sordaria fimicola (Rob.) Ces. & de Not.				0.56			
	Stagonospora sp.	0.56						
	Trichoderma aureoviride				1.67			
	Trichoderma harzianum		0.56		1.11	1.11	1.67	1.11

	Trichoderma koningii						0.56	
	Trichoderma piluliferum					0.56		1.11
	Trichoderma pseudokoningii				0.56			0.56
	Trichoderma viride		1.67		1.11	0.56	1.67	0.56
	Ulocladium botrytis Preuss					0.56		
	Verticillium balanoides (Drechsler) Dowsett, Reid & Hopkin				0.56			
S. planifolia roots	*Acremonium strictum*	0.71						
	Cladosporium herbarum		0.71	0.71				
	Fusarium chlamydosporum			1.43				
	Fusarium sporotrichioides Sherb.			1.43				
	Monocillium constrictum				2.14			
	Monocillium nordinii	0.71			0.71			
	Mortierella alpina						0.71	
	Mortierella elongata			0.71				
	Mortierella ericetorum	1.43						
	Mortierella minutissima		0.71	0.71				
	Mucor cf. mucedo					1.43		
	Mucor hiemalis	2.14	2.86	0.71	1.43	0.71	3.57	5.71
	Penicillium commune			0.71				
	Phialocephala dimorphospora				2.14	0.71		
	Phialocephala fortinii			0.71	2.14	0.71	2.86	
	Phialophora alba	1.43		1.43	2.86	2.86		2.86
	Phialophora cf. alba				0.71			
	Phialophora cyclaminis van Beyma	0.71						
	Phialophora melinii (Nannf.) Conant				0.71			
	Polyscytalum cf. hareae			0.71				
	Pycnidial sp. 3	0.71						
	Pycnidial sp. 6							0.71

Pycnidial sp. 7				0.71			
Rhizoctonia sp.					1.43		
Sporothrix sp. 2	0.71						
Trichoderma aureoviride						0.71	
Trichoderma harzianum			0.71	0.71			0.71
Trichoderma koningii	1.43		2.14			1.43	0.71
Trichoderma longibrachiatum	0.71						
Trichoderma piluliferum	0.71	1.43	1.43	0.71		0.71	
Trichoderma polysporum	2.14		2.14	0.71	0.71	0.71	0.71
Trichoderma pseudokoningii	2.14	1.43		0.71			
Trichoderma viride		2.14	2.14	3.57	2.14	1.43	0.71
Verticillium balanoides	1.43		0.71				

Table 4-3. Pearson's correlation coefficients among the Canonical correspondence axes and litter quality variables of decomposing *Sphagnum fuscum* from Perryvale bog and *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots from the riverine sedge fen in Alberta, Canada.

	Axis 1	Axis 2	TC	TN	TC:TN	TP
Axis 1	1.000					
Axis 2	0.046	1.000				
TC	-0.122	-0.286	1.000			
TN	-0.698 **	0.053	0.263	1.000		
TC:TN	-0.707 **	0.539 *	-0.251	-0.939 ***	1.000	
TP	0.919 ***	-0.382	-0.210	0.754 **	-0.723 **	1.000

TC = Total carbon, TN = total nitrogen, TC:TN = total carbon to total nitrogen quotient, TP = total phosphorus. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Table 4-4. Pearson's correlation coefficients among the Canonical correspondence axes and litter quality and surface water chemistry variables of decomposing *Sphagnum fuscum* from Perryvale bog, Alberta, Canada.

	Axis 1	Axis 2	TC	TP	pH	TP (H_2O)
Axis 1	1.000					
Axis 2	-0.034	1.000				
TC	0.823 ***	-0.076	1.000			
TP	0.579 *	-0.343	0.233	1.000		
pH	0.480	-0.826 **	0.587 *	0.506 *	1.000	
TP (H_2O)	-0.626 *	-0.289	-0.542 *	0.132	-0.026	1.000

TC = Total carbon, TP = total phosphorus, TP (H_2O) = surface water concentrations of total phosphorus. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Table 4-5. **Pearson's correlation coefficients among the Canonical correspondence axes and litter quality variables of decomposing *Carex aquatilis* leaves and rhizomes from the riverine sedge fen, Alberta, Canada.**

	Axis 1	Axis 2	TC	TN	TC:TN	TP
Axis 1	1.000					
Axis 2	0.031	1.000				
TC	0.020	0.030	1.000			
TN	0.159	-0.931 ***	0.192	1.000		
TC:TN	-0.095	0.940 ***	0.192	-0.975 ***	1.000	
TP	0.644 *	-0.564 *	-0.241	0.612 *	-0.638 *	1.000

TC = Total carbon, TN = toal nitrogen, TC:TN = total carbon to total nitrogen quotient, TP = total phosphorus. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Table 4-6. Pearson's correlation coefficients among the Canonical correspondence axes and litter quality variables of decomposing *Carex aquatilis* rhizomes and *Salix planifolia* roots from the riverine sedge fen, Alberta, Canada.

	Axis 1	Axis 2	TC	TN	TC:TN	TP
Axis 1	1.000					
Axis 2	0.002	1.000				
TC	-0.371	-0.918 ***	1.000			
TN	-0.832 **	-0.365	0.639 *	1.000		
TC:TN	0.844 **	0.222	-0.499 *	-0.958 ***	1.000	
TP	0.192	0.538 *	-0.624 *	-0.063	-0.078	1.000

TC = Total carbon, TN = toal nitrogen, TC:TN = total carbon to total nitrogen quotient, TP = total phosphorus. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

CHAPTER 5. EFFECTS OF TEMPERATURE ON DECOMPOSITION RATES OF THE DOMINANT VEGETATION OF SOUTHERN BOREAL PEATLANDS BY BACTERIA AND FUNGI

INTRODUCTION

Global warming due to increased atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4), and nitrous oxides (NO_X) could lead to increased atmospheric temperatures by the middle of the 21st century (IPCC 2001). Global climate models (GCM) predict that temperature increases will be more pronounced in northern continental regions during spring and winter months, with mean annual temperature increases ranging from 4 to 8 °C (Boer et al. 1992). These regions consist of a mosaic of boreal forests and peatlands. Peatlands cover approximately 4% of the world's and 14% of Canada's landscape (National Wetlands Working Group 1988). Approximately 16% of Alberta's land surface consists of peatlands (4.9% bogs and 11.4% fens) (Vitt et al. 1996).

Peatlands accumulate peat, which is a heterogeneous assemblage of partially decomposed plant material consisting of approximately 50% carbon (C) (Thormann et al. 1999). Gorham (1991) emphasized the importance of peatlands to the global C-cycle by estimating that northern peatlands store between 180 and 277 Gt C (1 Gt = 1×10^9 t), which represents approximately 10 to 16% of the total global terrestrial detrital C. It has been suggested that peat accumulates due to an imbalance of litter decomposition and net primary plant production (Clymo 1965, Malmer 1986, Farrish and Grigal 1988, Vitt 1990). Rates of C mineralization, or decomposition (measured as mass losses), in peatlands are sensitive to hydrology, oxygen availability, acidity, the nutrient status of the ecosystem, and temperature (Brinson et al. 1981, Bartsch and Moore 1985, Farrish and Grigal 1988, Gorham 1991, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a, Thormann et al. 2001). Litter quality, such as tissue concentrations of total nitrogen (TN) and total phosphorus (TP), also has been shown to affect rates of decomposition of plant litters in peatlands (Bridgham and Richardson 1992, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a, Thormann et al. 2001).

Fungi synthesize a diverse suite of enzymes, such as cellulases, polyphenol oxidases (PPO), pectinases, and amylases, that allow them to degrade a variety of organic materials (Deacon 1984). Many fungi have the ability to degrade simple molecules, such as starch; however, the ability of fungi to degrade complex structural polymers (lignins, tannins, and their derivatives) is uncommon (Domsch et al. 1980, Chapter 3, Appendix 3). The impact of increasing atmospheric temperatures on enzyme syntheses by fungi remains unclear, with some studies showing increased and other decreased activity of enzymes, such as cellulases and PPOs (Forbes and Dickinson 1977, Zadražil 1985, Widden et al 1989, Moorhead and Linkins 1997).

Elevated atmospheric CO_2 concentrations have the potential to alter leaf litter chemistry and hence decomposition, possibly altering C and N cycling in ecosystems (O'Neill and Norby 1996, Randlett et al. 1996). Although several studies have examined decomposition rates of leaf litters grown at ambient and elevated CO_2 concentrations, results were variable and depended on the experimental design, the litter used, and the length of the experiment among others (Melillo 1983, Rastetter et al. 1992, Randlett et al. 1996, Hirschel et al. 1997). Although temperature has been recognized as an important factor influencing rates of decomposition, its effects on microbial populations generally are poorly studied and only recently have received some attention (Carreiro and Koske 1992a, b, Kandeler et al. 1998, Bardgett et al. 1999). It has been suggested that fungi are the principal decomposer microbes in wetlands and assume a more dominant role than bacteria in the acrotelm (Latter et al. 1967, Williams and Crawford 1983), at least during the initial stages of decomposition (Newell et al. 1995, Kuehn et al. 2000). However, the majority of studies investigating C-dynamics in peatlands concentrate on bacterial populations and their role in the mineralization of C to produce CH_4 (Yavitt et al. 1993, Bubier et al. 1993). Furthermore, some studies simply do not address fungi as organisms involved in the decomposition of plant litters (Gilbert et al. 1998a) or have found them to be only minor components of the microbial community (Gilbert et al. 1998b). Very few studies have investigated the effects of elevated CO_2 concentrations on fungal decomposition in decomposing plant litters (Conway et al. 2000) and I could find none that examined rates of bacterial decomposition under these conditions. Furthermore, I could not find any reports in the literature that make direct comparisons of decomposition rates between the dominant bacteria and fungi of the same plant litter. Thus, the relative contribution of fungi and bacteria to the decomposition of plant litters remains unknown.

To elucidate the relative importance of fungi and bacteria in the decomposition of peatland plants under ambient and elevated atmospheric temperatures, I initiated an *in vitro* study comparing their relative abilities to decompose the dominant plant species of two southern boreal peatlands at two temperature regimes. These plant litters were *Sphagnum fuscum* (Schimp.) Klinggr. plants from a bog and *Carex aquatilis* Wahlenb. leaves and rhizomes from a riverine, sedge-dominated fen. These two plant species have been shown to contribute significantly to the total net primary plant production (Szumigalski and Bayley 1996b, Thormann and Bayley 1997b) and accumulation of peat in southern boreal peatlands (Kuhry and Vitt 1996, Thormann et al. 1999). I hypothesized that (1) fungi would cause larger mass losses of these litter types than bacteria, because fungi have faster growth rates and therefore would be able to colonize the plant litters more effectively than bacteria, (2) mass losses caused by fungi and bacteria would increase with increasing temperatures, because their rates of growth and enzyme synthesis generally are optimal between 20 and 30 °C, (3) mass losses of the litter types would be greatest when bacterial and fungal populations coexist, because of synergistic relationships between these microbial populations, and (4) mass losses of the *Carex* litters will exceed those of the *Sphagnum* litter, because of higher initial concentrations of total nitrogen and total phosphorus in the fen plants.

METHODS

Decomposition of *Carex aquatilis* leaves and rhizomes and *Sphagnum fuscum* plants *in situ*

Leaves and rhizomes of *Carex aquatilis* from a fen and the top 3 cm of whole *Sphagnum fuscum* plants from a bog were collected in early September 1997. Senesced leaves and live rhizomes of the sedge were cut into 5 cm segments. All segments were used for the decomposition study, irrespective of their position within an individual leaf or rhizome. A decomposition study using nylon mesh bags (3 x 6 cm, 1 mm gauge) was initiated that fall (Thormann et al. 2001). Briefly, 3.0-5.0 g fresh weight of each litter type were placed into individual decomposition bags and subsets of triplicate decomposition bags were retrieved after 20 and 50 days in 1997, after eight and 12 months in May and September 1998, and after 20 and 24 months in May and September 1999.

Isolation of fungi

All decomposed litters were cleaned by removing roots and other plant tissues using fine forceps and a dissecting microscope. Each of ten randomly selected, cleaned segments of *Carex aquatilis* leaves and rhizomes and *Sphagnum fuscum* plants was cut with a flame-sterilized scalpel into ten smaller segments (approximately 5 x 5 mm in size). These were surface-sterilized for five minutes in 10% hydrogen peroxide (H_2O_2) and washed with sterilized, distilled water (d-H_2O). Five randomly selected segments of each litter type were placed on each of three plates of Potato Dextrose Agar (PDA, 39.0 g Difco potato dextrose agar, 1.0 L d-H_2O), PDA with rose bengal (0.03%), PDA with benomyl (0.0002%), and Mycobiotic agar® (MYC, containing cycloheximide, 35.6 g Difco mycobiotic agar, 1.0 L d-H_2O) for the isolation of fungi. All media were amended with oxytetracycline (0.01%) to suppress bacterial growth. Plates were incubated at room temperature in the dark and fungi were sub-cultured onto Malt Extract Agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) as soon as they grew from the plant material. For identification purposes, slide cultures (Sigler 1993) on mixed cereal agar (CA, Pablum®, H. J. Heinz Company of Canada Ltd., 100.0 g mixed cereal, 15.0 g Difco agar, 1.0 L d-H_2O) were prepared, mounted in polyvinyl alcohol, and photographed using an Olympus BX-50 microscope with a PM-10AK photosystem.

Isolation of bacteria

Senesced leaves and live rhizomes of *Carex aquatilis* and the top 3 cm of whole *Sphagnum fuscum* plants were collected in early September 2000. These tissues were cleaned and sterilized as outlined above. Approximately 3.0 g fresh weight of each litter type were placed into 100 mL sterilized phosphate buffer (P-buffer, pH = 7.25, 10 mM) and homogenized in a Sorvall Omni-Mixer (Norwalk, CT) at speed setting "5" for five minutes. A serial dilution of each homogenate in P-buffer was performed to obtain final concentrations of 1×10^{-3} to 1×10^{-8} of homogenized plant material prior to transferring 0.2 mL of each dilution concentration onto plate count agar (PCA, 23.5 g Difco plate count agar, 1.0 L d-H_2O, final pH 7.0). The transferred solution was spread over the agar with a flame-sterilized, bent glass rod. Triplicate plates of each litter type at each dilution concentration were incubated at room temperature in the dark and monitored daily for the appearance of bacterial colonies. The three most common bacteria of each litter type, as determined by morphological (shape, size, and colony colour) and physiological (ability to grow on various bacteriological growth media) characteristics were sub-cultured onto PCA. These bacteria were identified to genus following Sneath et al. (1986) (Table 5-1).

Experimental design

Preparation of microcosms

I selected the three most common fungal and bacterial taxa that were isolated from senesced plant material of each litter type for the *in vitro* decomposition study (Table 5-2). All fungi and bacteria were grown on peptone broth agar (PBA, 20.0 g Difco agar, 1.0 g Difco bacto-peptone broth, 1.0 L d-H_2O) for ten days at 14 °C and 20 °C in the dark prior to the experiment to determine the suitability of this medium. PBA was chosen as it provided some N, other than the N from the plant litters themselves, to the fungi and bacteria. These conditions are similar to those *in situ*, where microbial populations have access to sources of nutrients other than the litter they are colonizing and decomposing.

PBA was poured into 10 x 80 mm plastic petri plates. Triplicate plates were inoculated with the indigenous fungi of each litter type by themselves and in every possible combination with each other. Plates were inoculated by transferring two mycelial plugs (1.0 x 1.0 x 0.5 mm) onto the appropriate treatment plates. For each bacterium, a suspension was prepared by transferring the bacterial colonies of one-week old cultures into 30 mL sterilized P-buffer in sterilized Pyrex culture tubes. P-buffer was chosen as a suspension medium for the bacteria as it maintains the bacteria in an osmotic equilibrium, thereby keeping them alive during the inoculation procedure. These suspensions were vortexed for 10 sec. at setting “5” prior to the inoculations (0.2 mL treatment^{-1}) of each litter type. As with the fungi, three bacteria indigenous to each litter type were inoculated onto the appropriate PBA plates by themselves and in every possible combination with each other. All fungal treatments also received 0.2 mL P-buffer. Triplicate petri plates were inoculated simultaneously with all three indigenous fungi and bacteria of each litter type to investigate possible synergistic relationships among the fungi and bacteria during the process of decomposition. Uninoculated plates served as controls to determine mass losses of these litters due to leaching. A total of 384 petri plates were set up for each litter type ([seven treatments each of fungi and bacteria + one fungi plus bacteria treatment + control] x three replicates each x four decomposition periods x two temperature treatments).

Decomposition of *Sphagnum fuscum* plants and *Carex aquatilis* leaves and rhizomes

Polyester mesh pouches (2.5 x 3.0 cm, 65 µm gauge) contained the top 3 cm of four dried *Sphagnum fuscum* plants to minimize plant material losses during handling. The dried *Carex aquatilis* litters were not placed into polyester pouches, as losses during handling were not anticipated. The pouches and the dried sedge litters were weighed to the nearest 0.01 g and autoclaved at 121 °C (liquid cycle) for 15 minutes prior to placement into the petri dishes, at which time they were inoculated with the appropriate fungi and bacteria. Autoclaving did not alter the morphological structure of the plant material; however, molecular changes within plant cells likely occurred (Tsuneda et al. 2001). Alternate sterilization techniques, such as gamma-irradiation, may be less invasive and decrease intracellullar changes within the plant litters. Half of the plates were incubated at 14 °C (ambient mean annual growing season temperature, May-October, Athabasca 2 weather station) (Environment Canada 1998), while the other half was incubated at 20 °C (predicted 6 °C increase of the mean annual growing season temperature at northern latitudes under a 2 x CO_2 scenario) (Boer et al. 1992, IPCC 2001).

After two, four, eight, and 12 weeks, the litters were removed from three petri dishes for each litter type and surficial fungal mycelium was carefully removed with forceps from the pouches or the surface of the leaves and rhizomes. The litters were dried at 48 °C to constant mass, weighed to the nearest 0.01 g, and mass losses were determined by subtracting the final mass from the initial mass. Mass losses were expressed as percentages of the initial masses. Bacterial and fungal biomass of the litters were not determined.

Mean mass losses of these three litter types due to leaching of soluble and small-molecular mass compounds were 1.9% for *Sphagnum fuscum*, 9.1% for *Carex aquatilis* rhizomes, and 15.0% for *C. aquatilis* leaves *in vitro*. These mass losses were subtracted from all data prior to statistical analyses.

Enzymatic degradation of selected carbon sources

Cellulose degradation was tested using the cellulose-azure method (Smith 1977) with modified Melin-Norkrans medium (MMN, 1.0 g d-glucose anhydrous, 2.0 g Difco malt extract agar, 1.0 g yeast extract, 10.0 g KH_2PO_4, 5.0 g $(NH_4)_2HPO_4$, 3.0 g $MgSO_4 \cdot 7H_2O$, 1.0 g $CaCl_2$, 0.5 g NaCl, 12.0 g Difco agar, and 1.0 L d-H_2O). Approximately 20 mL of MMN were added to 50 mL Pyrex culture tubes, these were autoclaved, and the medium was allowed to solidify. A 2% (w v^{-1}) cellulose-azure preparation in MMN was autoclaved separately and approximately 1.5-2.0 mL of the suspension was aseptically transferred into each Pyrex culture tube. Degradation of cellulose was indicated by the release of the azure dye from the cellulose agar and its diffusion into the lower, clear layer of MMN. For each fungal taxon, three Pyrex culture tubes with cellulose-azure medium were inoculated with small plugs of mycelium and stored under ambient light and temperature conditions on the laboratory bench.

The presence of PPO, the enzymes required for lignin degradation, was tested using tannic acid medium (TAM, 5.0 g Tannic acid [Baker analyzed], 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) (Davidson et al. 1938). For each fungal taxon, five petri plates of TAM were inoculated and stored in the dark at room temperature. A positive reaction was the formation of a dark brown pigment surrounding the point of inoculation generally within four days after inoculation.

Starch degradation was tested by adding 2.0 g of soluble starch (BDH Chemicals Canada Ltd., Toronto, Canada) to 1.0 L MMN (Hutchison 1990). Once the individual colonies covered approximately 75% of the petri plates, they were flooded with an iodine solution (5.0 g KI, 1.5 g I, 100.0 mL d-H_2O). After five minutes, the solution was decanted and a clear zone surrounding the colony in an otherwise purple plate indicated that amylase was produced and starch was degraded.

Citrus pectin (5.0 g, Sigma Chemical Co., U.K.) was added to 1.0 L MMN (Hutchison 1990). The medium was heated and stirred prior to autoclaving in order to dissolve completely the pectin. Petri plates were flooded for 6 hours with a 1% aqueous solution of hexadecyltrimethylammonium bromide (Sigma Chemical Co., St. Louis, MO). Following decanting of the solution, pectinase activity was detected by the presence of a clear zone surrounding the fungal colony in an otherwise opaque background.

MMN with 120.0 g gelatin (Type B, from bovine skin, Sigma Chemical Co., St. Louis, MO) instead of agar was prepared (Hutchison 1990). The gelatin was added to 900.0 mL d-H_2O, dissolved, and autoclaved separately from the remaining ingredients, which were dissolved in 100.0 mL d-H_2O. Both solutions were mixed prior to pouring into petri dishes. The medium liquefies around and below the fungal colony if gelatinase is synthesized.

I did not test the bacteria for their abilities to degrade these C sources. Physiological data and optimal growth rate temperatures for the bacterial genera can be found in Sneath et al. (1986).

RESULTS

Mass losses caused by fungi and bacteria

Mass losses of each litter type caused by the fungi ranged from 0.5 to 12.3% after 12 weeks (Table 5-3). Specifically, mass losses of the *Sphagnum fuscum* litter caused by the fungi were significantly greater at 14 than at 20 °C (2.4 *vs.* 0.5%, respectively) ($p < 0.05$). In contrast, the three most common indigenous fungi of the *Carex aquatilis* leaf and rhizome litters caused significantly greater mass losses at 20 than at 14 °C (Table 5-3) ($p < 0.05$). While mass losses nearly doubled for the *C. aquatilis* rhizome litter, they increased nearly 31-fold for the *C. aquatilis* leaf litter under the increased temperature regime (Table 5-3). Generally, mass losses of the sedge litters were greater than those of the bryophyte litter at either temperature (Table 5-3).

Mass losses of each litter type caused by bacteria ranged from 0.2 to 7.3% after 12 weeks (Table 5-3). The indigenous bacteria of *Sphagnum fuscum* caused significantly greater mass losses at 14 than at 20 °C (3.2 *vs.* 0.2%, respectively). Conversely, mass losses of the *Carex* *aquatilis* leaf litter by its three most common indigenous bacteria were significantly greater at 20°C ($p < 0.05$). No trend was apparent in the *C. aquatilis* rhizome litter, where mass losses caused by bacteria were similar at both temperatures ($p > 0.05$) (Table 5-3).

In comparison, mass losses caused by fungi were up to three times greater than those caused by bacteria for each of these plant litters at 20 °C ($p < 0.05$) (Table 5-3). At 14 °C, bacterial mass losses significantly exceeded fungal mass losses in the *Sphagnum fuscum* litter ($p < 0.05$). Conversely, fungal mass losses significantly exceeded bacterial mass losses of the *Carex aquatilis* leaf litter ($p < 0.05$). Fungal and bacterial mass losses were similar for the *C. aquatilis* rhizome litter ($p > 0.05$) (Table 5-3).

When the three most common indigenous fungi and bacteria of each litter type were combined, mass losses of both sedge litters generally were significantly greater at both temperatures (Table 5-3). This was not the case for the *Sphagnum fuscum* litter, where bacterial plus fungal mass losses were similar to those caused by the three most common fungi or bacteria by themselves (Table 5-3). The greatest mass losses were those of *Carex aquatilis* rhizomes (mean of 25.3% at both temperatures) (Figure 5-1, Table 5-3).

In some cases, the litters apparently had gained mass after 12 weeks (Figure 5-2, Table 5-3). These mass gains were as high as 3.2% above the initial mass of the litter. Furthermore, a distinct pattern of mass losses occurred over the 12-week decomposition period. Mass losses after two weeks were often significantly higher than those after four and eight weeks and similar to or less than those at the end of the decomposition period (Figures 5-1, 5-2).

In situ mass losses of *Sphagnum fuscum*, *Carex aquatilis* leaves, and *C. aquatilis* rhizomes were 19.4, 26.3, and 45.3%, respectively, after 12 weeks (Thormann et al. 2001, Chapter 2). If the current leaching mass losses of each litter types were subtracted from their *in situ* mass losses, mass losses caused by microbial communities were 17.5% for *S. fuscum*, 11.2% for *C. aquatilis* leaves, and 36.2% for *C. aquatilis* rhizomes after 12 weeks *in situ*.

Mass losses caused by individual fungi and bacteria

For *Sphagnum fuscum*, *Trichoderma viride* and *Penicillium thomii* (both 2.2% at 14 °C) caused the greatest mass losses over the 12-week decomposition period, while *Brevibacterium* sp. (4.5% at 14 °C) caused the greatest mass losses by the bacteria over the same period. When combined, *Mucor hiemalis* plus *T. viride* (4.4% at 14 °C) and *Bacillus* sp. 2 plus *Arthrobacter* sp. 3 (4.4% at 14 °C) caused the greatest mass losses of this bryophyte after 12 weeks. For *Carex aquatilis* rhizomes, *Phialocephala dimorphospora* (28.4% at 20 °C) and *Arthrobacter* sp. 1

(8.0% at 20 °C) caused the greatest mass losses after 12 weeks. In combination, *M. hiemalis* plus *P. dimorphospora* (24.6% at 20 °C) and *Arthrobacter* sp. 1 plus *Leuconostoc* sp. 1 (4.1% at 20 °C) caused the greatest mass losses of *C. aquatilis* rhizomes over the 12-week period. For *C. aquatilis* leaves, *Monocillium constrictum* (10.6% at 20 °C) and *Bacillus* sp. 1 (8.0% at 14 °C) were the most successful fungus and bacterium, respectively, degrading this litter type. When combined, basidiomycete sp. 3 plus *M. constrictum* (24.8% at 20 °C) and *Arthrobacter* sp. 2 plus *Bacillus* sp. 1 (10.4% at 20 °C) caused the greatest mass losses of the *C. aquatilis* leaf litter. Mass losses by the remaining fungi and bacteria of each litter, alone and in combination, were less than those above (data not shown). In some cases, the litters gained weight during the 12-week decomposition period (Table 5-3). Weight gains were between 0.1 to 9.1% for fungi and bacteria by themselves and in combination with each other.

Enzymatic abilities of the fungi and growth rates

The nine fungi varied in their ability to degrade the five different C sources (Table 5-4). All fungi were able to degrade gelatin. Only *Monocillium constrictum* and *Phialocephala dimorphospora* were able to utilize tannic acid as a C source (Table 5-4). Both species of *Penicillium* and *P. dimorphospora* showed significantly slower growth rates at 14 °C than at 20 °C ($p < 0.01$) over the first ten days. Growth rates of the remaining five fungal taxa were not inhibited significantly by the lower incubation temperature ($p > 0.05$) (Table 5-4).

DISCUSSION

Effects of different microbial populations on mass losses

Mass losses

Some litters experienced mass gains during the decomposition process (Figure 5-2, Table 5-3), possibly because the microbial biomass within the litter exceeded mass losses due to decomposition. Furthermore, the substantial mass losses observed within the first two weeks of decomposition often were significantly higher than those measured after four and eight weeks (Figures 5-1, 5-2). It is likely that these fungi and bacteria preferentially utilized low-molecular weight compounds during the initial colonization phase of the litters, resulting in high initial mass losses. Subsequently, the relative proportion of more recalcitrant structural polymers, such as lignin and cellulose, increased relatively to the smaller molecular-weight compounds. After this initial phase, fungi and bacteria continued to colonize the plant litter and increased their biomass, resulting in mass gains and ultimately lower measured mass losses as increases in microbial biomass were greater than decomposition mass losses. During the latter stages of decomposition, all labile compounds may have been depleted and the fungi and bacteria began to degrade structural polymers, resulting in net mass losses (Figures 5-1, 5-2) as increases of microbial biomass were less than decomposition mass losses.

Fungi

Differences in observed mass losses by these fungi may have been due to litter quality, temperature, and physiological variables. Both species of *Trichoderma* showed the same enzymatic abilities and growth rates *in vitro* (Table 5-4); however, they caused significantly different mass losses of the bryophyte and sedge rhizome litters (means of 0.9 and 7.2% respectively, at both temperature regimes). Initial TN and TP tissue concentrations differed significantly between these two litters (Thormann et al. 2001), with the bryophyte litter poorer in both nutrients. The same trend was observed for both species of *Penicillium* decomposing *S. fuscum* and *C. aquatilis* leaves. *Phialocephala dimorphospora* and *Monocillium constrictum* caused the largest mass losses of any of the fungi at 20 °C (28.4 and 10.6%, respectively), possibly because these two fungi were the only ones able to synthesize PPOs to utilize polyphenolics, such as tannic acid and lignin (Table 5-4). These compounds constitute a major component of plant litters, often comprising up to 35% of structural polymers. However, both fungi showed significant decreases of growth at lower temperatures (Table 5-4) and the mass losses they caused were lower than or similar to those of other fungi in this study at 14 °C (data not shown).

Although synergistic relationships among fungi may enhance decomposition of some substrates via sequential or simultaneous colonization and decomposition of plant litters, this is not always the case. Some fungi, such as species of *Trichoderma*, are mycoparasites and obtain nutrients by parasitizing other fungi (Deacon 1984). These interactions affect colonization strategies and competitive interactions among fungi, thereby influencing decomposition rates of natural substrates.

Mucor hiemalis was used to decompose *Sphagnum fuscum* and *Carex aquatilis* rhizomes and its ability to decompose either litter type depended on temperature. This zygomycete showed decreased decomposition rates with increasing temperatures in the bryophyte litter (1.8% at 14 °C to 0.0% at 20 °C) and increasing decomposition rates with increasing temperatures in the rhizome litter (5.4% mass gains at 14 °C to 4.2% mass losses at 20 °C), irrespective of the initial litter quality. Litter with comparatively high initial TN and TP tissue concentrations may not necessarily decompose faster than litter with lower initial TN and TP tissue concentrations. Temperature may ultimately supercede litter quality and enhance mass losses by fungi of some litters and not others. It must be noted though, that different fungi likely will respond differently and generalizations about the responses of fungi to the possible interaction between temperature and litter quality during the process of decomposition can not be drawn from these data.

Bacteria

Distinct differences in the ability of the indigenous bacteria to decompose their respective litters were apparent, with maximum mass losses of 8.0% (*Arthrobacter* sp. 2) for individual bacteria to 9.8% for the three most common bacteria decomposing *Carex aquatilis* rhizomes (Figure 5-1) after 12 weeks. Species of *Micrococcus* (Christensen and Cook 1970, Given and Dickinson 1975, Golovchenko et al. 1994), *Bacillus* (Latter et al. 1967, Christensen and Cook 1970, Given and Dickinson 1975, Martin et al. 1982, Golovchenko et al. 1994), and *Arthrobacter* (Latter et al. 1967, Christensen and Cook 1970, Martin et al. 1982) represent some of the most common bacteria isolated previously from peatlands. These bacteria are strict aerobes or facultative anaerobes with optimal growth temperatures between 20 and 30 °C (Sneath et al. 1986). The diversity of bacteria in peatlands has been shown to be restricted (Latter et al. 1967, Williams and Crawford 1983) due to sub-optimal pH levels in most peatlands (Baker 1970, Hiroki and Watanabe 1996). Nonetheless, bacteria have diverse physiological abilities and are able to utilize a wide variety of substrates, ranging from lignin to cellulose to simple sugars (Williams and Crawford 1983). Furthermore, synergistic relationships among bacteria to utilize organic substrates in organic soils have been suggested by Christensen and Cook (1970). To my knowledge, the remaining bacterial genera, *Leuconostoc*, *Lactobacillus*, and *Brevibacterium*, have not been isolated from peatlands previously; however, they have similar oxygen and temperature requirements as the previously discussed bacteria (Sneath et al. 1986).

Effects of temperature on the microbial community, biomass, and enzyme synthesis

Distinct differences in the ability to decompose the three plant litters at 14 and 20 °C were shown by these fungi and bacteria. Mass losses of fungi exceeded those of bacteria at 20 °C with no trend being apparent at 14 °C (Table 5-3), indicating that decomposition dynamics of fungi and bacteria differ and were temperature-dependent. Although the microbial community, its biomass, and the effects of temperature on enzyme synthesis were not determined in this study, all three have been shown to be sensitive to atmospheric temperatures.

Microbial community composition

Numerous studies have shown positive correlations between rates of decomposition of plant litters and temperature in peatlands (Clymo 1965, Brinson et al. 1981, Lieffers 1988, Bridgham and Richardson 1992). Furthermore, several studies have examined the effects of increasing atmospheric temperatures on microbial communities and their roles in ecosystems processes, such as decomposition, nutrient turnover, and energy flow (Widden and Hsu 1987, Carreiro and Koske 1992a, b, O'Neill 1994, Schlesinger 1995, Soussana et al. 1996, Trumbore et al. 1996, Zogg et al. 1997, Kandeler et al. 1998).

Anderson (1992) suggested that increases in atmospheric temperatures may affect soil microbial communities (1) by increasing rates of plant production and therefore the amount of substrate available for microbial communities and (2) by providing more favourable conditions for microbial growth and activity. Carreiro and Koske (1992a) determined that temperature had significant effects on the species composition and structure of microfungal communities isolated from decomposing leaf litters at 0, 10, and 20 °C. As temperatures increased, fungi imperfecti became more dominant while zygomycetes became less dominant in their decomposing leaf litters. Furthermore, although species richness remained similar across their temperature range, species diversity increased with increasing temperatures. Carreiro and Koske (1992a) determined that temperature and moisture affected fungal communities throughout the year within an ecosystem. As these variables change, the competitiveness of individual fungi and their community (Widden and Hsu 1987), as well as use (MacDonald et al. 1995, Zogg et al. 1997) and colonization patterns of natural substrates (Widden 1984, Carreiro and Koske 1992a) change as well. For example, increases in temperature impose physiological limits on and control rates of spore germination, growth, reproduction, and enzyme synthesis of fungi (Griffin 1981, Kendrick 1985, Zogg et al. 1997), thereby affecting competitive interactions among them (Widden 1984, Widden and Hsu 1987, Carreiro and Koske 1992b).

Microbial biomass

The effects of temperature on microbial biomass ~~are~~ variable. Bardgett et al. (1999) found that an increase of 2 °C resulted in an increase in active microbial biomass in their N-limited model terrestrial ecosystem without an increase in plant biomass or soil C-availability, suggesting that the soil microbial community responded directly to the temperature increase rather than indirectly to a change in plant productivity. Similar results were obtained by O'Neill (1994). However, their results are in conflict with those of Tinker and Ineson (1992) and

Kandeler et al. (1998) who argued that small temperature shifts of 1 - 2 °C may have no effect on microbial communities and total microbial biomass, because many microbes have broad temperature optima. However, atmospheric temperatures are predicted to increase between 4 and 8 °C at northern latitudes (Boer et al. 1992) and these temperature increases may be substantial enough to affect microbial populations and their roles in ecosystems. Ultimately though, the nutrient status of the ecosystem may determine the effects of increasing temperatures on microbial biomass (Klironomos et al. 1996, Randlett et al. 1996, Kandeler et al. 1998). Although soil microbes are thought to be C-limited (Zak et al. 1993), these studies have shown that increases in soil N-availability generally resulted in increases in total soil microbial biomass.

Enzyme synthesis

The effects of increasing atmospheric temperatures on the enzymatic ability of fungi remain uncertain, with some fungi showing increases and others decreases in enzymatic activities (Forbes and Dickinson 1977, Zadražil 1985, Widden et al. 1989, Moorhead and Linkins 1997). However, Freeman et al. (2001) suggested that global warming may lead to the rapid decay of peat, because of the increased activity of (poly)phenol oxidases under aerobic conditions. PPOs are the enzymes required to decompose phenolic compounds, such as lignins, tannins, and lignin-like compounds. However, their hypothesis fails to address the origin of the PPOs in the peat. The ability of fungi (other than most basidiomycetes) and bacteria to synthesize PPOs is limited (Domsch et al. 1980, Chapter 3, Appendix 3), likely due to the complex molecular nature of phenolic compounds, which requires a suite of different enzymes rather than a single enzyme to mineralize them.

For example, less than 13% of all fungi isolated from living and decomposing *Sphagnum fuscum* were able to utilize tannic acid as a C source, whereas the same fungi utilized cellulose (49%), starch (45%), and pectin (24%) to a much higher degree (Chapter 3). What these percentages may be for the suite of fungi *in situ* remains unknown; however, I hypothesize them to be similar to those observed in this study. Similarly, few bacteria have the ability to synthesize phenol oxidases (Cerniglia 1992). Furthermore, fungal degradation of substrates is extracellular, while bacterial degradation is an intracellular process that requires the bacterium to take up the substrate to be mineralized and enzymatically degrade it in the cell interior. This makes fungi the principle decomposers of these recalcitrant phenolics, because the molecular complexity and size of phenolic compounds prohibits bacteria from effectively decomposing them in nature. Only two of the eight fungi in this study had the ability to degrade tannic acid

(*Monocillium constrictum, Phialocephala dimorphospora*), while five or more were able to degrade the remaining four C-sources (Table 5-4). Therefore, the microbial community of peatlands may have a limited ability to decompose phenolic compounds, which constitute 27-55% of peat and become more prevalent with increasing peat depths (Turetsky et al. 2000).

Effects of litter quality on bacterial and fungal decomposition dynamics

The indigenous bacteria and fungi of the three plant litters caused significant differences in mass losses over the 12-week decomposition period (Table 5-3). It was surprising that the bryophyte mass losses exceeded those of the sedge leaf litter at 14 °C, because the sedge leaf litter had significantly higher initial TN and TP tissue concentrations than the bryophyte litter (TN: 201 *vs.* 68 mg g^{-1}; TP: 182 *vs.* 50 mg g^{-1}) (Thormann et al. 2001). Litter quality, such as tissue concentrations of TN and TP and TN:TC quotients, is a significant factor influencing decomposition rates of peatland plant species, whereby litters with higher TN and TP tissue concentrations generally decompose at faster rates (Brinson et al. 1981, Bridgham and Richardson 1992, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a, Thormann et al. 2001). However, the losses reported here were based on laboratory experiments, whereas *in situ* mass losses of these litters over the first 12 weeks of decomposition were significantly different: 45.3% for *C. aquatilis* rhizomes, 26.3% for *C. aquatilis* leaves, and 19.4% for *S. fuscum* (Thormann et al. 2001, Chapter 2). However, those mass losses include losses due to leaching of soluble compounds. Once leaching mass losses were subtracted from *in situ* mass losses, mass losses caused by the enzymatic activity of these fungi and bacteria were substantially lower, with those of the bryophyte exceeding those of the sedge leaves (17.5 *vs.* 11.2%) (Table 5-3).

In situ mass losses of these three litters were significantly higher than those measured *in vitro* (Table 5-3). Only three fungi and bacteria decomposed the litters in this study; however, a suite of fungi and bacteria decompose organic materials in nature. Therefore, higher mass losses of these litters *in situ* were not surprising. However, mass losses of *Carex aquatilis* leaves at 20 °C were similar to those observed *in situ* (Table 5-3). This litter type had the highest leaching mass losses at either temperature treatment (mean of 15.1%). The sedge litter was collected in early September and, although appearing senesced, may still have had substantial concentrations of tissue nutrients that had not been translocated into the rhizomes, thereby losing significantly higher quantities of soluble and small-molecular compounds than the bryophyte and rhizome litters due to leaching. Furthermore, *Phialocephala dimorphospora* was one of the most common fungi isolated from the rhizome litter (Table 5-2) and degraded tannic acid (Table 5-4). This ability may have contributed to the significant mass losses observed *in vitro* (Table 5-3).

Effects of temperatures on litter quality

I could not find any studies that examined the effects of elevated atmospheric temperatures on litter quality; however, a latitudinal gradient can be used as a proxy for a temperature gradient. Bernard et al. (1988) found that different species of *Carex* had similar mean summer aboveground tissue nutrient concentrations of N (mean of 14 mg g^{-1}, range of 6 to 21 mg g^{-1}) and P (1.3 mg g^{-1}, range of 0.3 to 2.0 mg g^{-1}). Their and additional data covered a range of wetlands from approximately 48 to 70° N (Small 1971, Chapin III et al. 1975, Auclair 1977, Klopatek 1978, Bernard and Hankinson 1979, Chapin III et al. 1988, Thormann and Bayley 1997c), which suggests that tissue nutrient concentrations of N and P in species of *Carex* are not significantly affected by temperature or ecosystem variability.

Tissue nutrient concentrations of belowground tissues of wetland plants are rarely reported, with concentrations ranging from 1 to 7 mg g^{-1} N and 0.2 to 1.3 mg g^{-1} P (Bernard and Solsky 1977, Klopatek 1978, Bernard and Hankinson 1979). Above- and belowground tissues nutrient concentrations of N and P in species of *Carex* in southern boreal Alberta wetlands fall within the ranges reported in the literature (Thormann and Bayley 1997c, Thormann et al. 2001).

I could not find any comparative studies examining rates of decomposition of plant tissues grown at different temperatures, possibly due to the absence of significant variations in the litter quality.

Effects of CO_2 concentrations on litter quality

Several studies have examined the effects of increasing atmospheric CO_2 concentrations on plant tissue nutrient concentrations (Randlett et al. 1996, Hirschel et al. 1997, Conway et al. 2000). For example, Randlett et al. (1996) determined that increasing atmospheric CO_2 concentrations resulted in a decrease of soluble sugar concentrations in *Populus* sp. leaf litter, while Curtis et al. (1989) measured decreases in green leaf tissue concentrations of N and a resultant increase in the C:N quotient in marsh plant species. Conversely, Hirschel et al. (1997) did not find significant changes in leaf litter tissue concentrations of C, N, and lignin in a variety of alpine, temperate, and tropical plant species. Therefore, although it has generally been assumed that nutrient tissue concentrations will be reduced at elevated atmospheric CO_2

concentrations (Lamborg et al. 1983, Strain and Bazzaz 1983, O'Neill and Norby 1996), results are variable and largely depend on the experimental design and plant species examined.

Similarly, results of studies of decomposition dynamics of plants grown at elevated atmospheric CO_2 concentrations by microbial communities are variable. Kemp et al. (1994), O'Neill and Norby (1996), and Hirschel et al. (1997) found no significant changes in decomposition rates between plants grown at ambient and elevated atmospheric CO_2 concentrations, while Coûteaux et al. (1991), Cotrufo et al. (1994), and Boerner and Rebbeck (1995) measured decreased rates of decomposition of plants grown at elevated atmospheric CO_2 concentrations. Therefore, much uncertainty remains in elucidating the effects of elevated atmospheric CO_2 concentrations and temperature on plant species litter quality and the effects on microbial communities involved in the decomposition of these plant species.

Implications for global warming

Despite disagreements in some of the predicted impacts of increasing atmospheric CO_2 concentrations, all GCMs predict increases in atmospheric temperatures in most areas currently covered by peatlands in Canada (IPCC 2001). In conjunction with lowered water levels in peatlands, these ecosystems are predicted to increase emissions of CO_2 due to increased rates of decomposition of peat in the acrotelm, thereby altering the C sink/source function of peatlands whereby peatlands may provide a positive feedback to climate warming (Gorham 1991, Bridgham et al. 1995).

Several studies have investigated microbial communities in wetland soils and plants and it has been suggested that fungi are the principal decomposer microbes and assume a more dominant role than bacteria (Latter et al. 1967, Williams and Crawford 1983, Newell et al. 1995, Kuehn et al. 2000). Furthermore, the relative importance of fungal to bacterial communities changes during the process of decomposition (Tanaka 1991) and distinct patterns of microbial succession have been observed in a variety of plant litters (Bärlocher and Kendrick 1974, Suberkropp and Klug 1974, 1976, Chapter 4). Nonetheless, temperature, moisture availability, and nutrients, all variables predicted to change directly or indirectly due to global warming, play major roles in microbial community composition, competition dynamics among microbial populations, microbial biomass, substrate accessibility and colonization patterns, and ultimately decomposition (Bissett and Parkinson 1979, Widden and Hsu 1987, Carreiro and Koske 1992a, b, O'Neill 1994, Schlesinger 1995, Randlett et al. 1996, Soussana et al. 1996, Trumbore et al. 1996, Zogg et al. 1997, Kandeler et al. 1998). Clear conclusions regarding the impact of increasing atmospheric temperatures on microbial communities and their functions in ecosystems can not be drawn due to conflicting results. The results of this study further underline the complexity of microbial interactions during the process of decomposition of plant materials. Furthermore, Bridgham et al. (1999) and Weltzin et al. (2000) showed that the vegetation of northern peatlands responds differently to warming and water table fluctuations. Above- and belowground processes control energy fluxes to some degree in peatlands, suggesting that biogeophysical dynamics of ecosystems may be as important as their biogeochemistry in response to global warming. Microbial community dynamics play a significant role in biogeochemical feedbacks, affecting nutrient pools and turnover rates of recalcitrant materials, which in turn affects the plant community (Bridgham et al. 1999).

Although GCMs have become more refined and incorporate an increasing number of variables to predict future climate changes and impacts on a variety of ecosystems, they have only incorporated abiotic variables thus far, because biotic variables are difficult to define and standardize for inclusion into GCMs. As Gorham (1994) pointed out, microbiological and biogeochemical studies rarely have, if ever, been linked in field studies and their relationships remain mostly speculative. These relationships need to be investigated to understand the effects of abiotic variables, such as increasing temperatures or lowered water levels, on biotic variables, such as fungal and bacterial community dynamics and their effects on decomposition processes.

CONCLUSIONS

Rates of decomposition of *Carex aquatilis* leaves and rhizomes from a fen and *Sphagnum fuscum* plants from a bog by fungi and bacteria were measured at 14 and 20 °C over a 12-week period *in vitro*. Mass losses of these plant litters by fungi were generally greater than those by bacteria at 20 °C; however, there were no clear trends at 14 °C, suggesting that hypothesis 1 should be rejected, because mass losses of fungi did not consistently exceed those of bacteria. Hypothesis 2 predicted that increasing temperatures would lead to increased mass losses of the three litter types. However, an increase in temperature did not always result in increased mass losses by fungi, bacteria, and fungi plus bacteria, and hypothesis 2 was thereby rejected. Furthermore, I hypothesized that mass losses would increase significantly when the most common bacteria and fungi were combined to decompose each of these litters (hypothesis 3). However, combining fungi and bacteria only resulted in significantly increased rates of decomposition at either temperature regime in three of the six treatments, suggesting that synergistic relationships among microbial communities occurred in some treatments but not others. Therefore, this hypothesis also had to be rejected. Lastly, I hypothesized that sedge litter mass losses would be significantly greater than those of the bryophyte. However, mass losses of the *Carex* litters did not consistently exceed those of the bryophyte litter. At 14 °C, mass losses of *S. fuscum* exceeded those of *C. aquatilis* leaves; however, they were significantly lower than those of either *Carex* litter type at 20 °C. Therefore, hypothesis 4 also was rejected. These data indicate the complexity of microbial interactions and roles and general conclusions about the functions of these microbes and those of natural systems can not be drawn. The influence of bacteria and fungi and their interactions during the decomposition of the dominant peatland plant species varied among litter types and different microbial populations respond differently to elevated atmospheric temperatures, suggesting that rates of C mineralization by fungi and bacteria in the acrotelm of peatlands under a global warming scenario will vary among different peatland types and plant litters.

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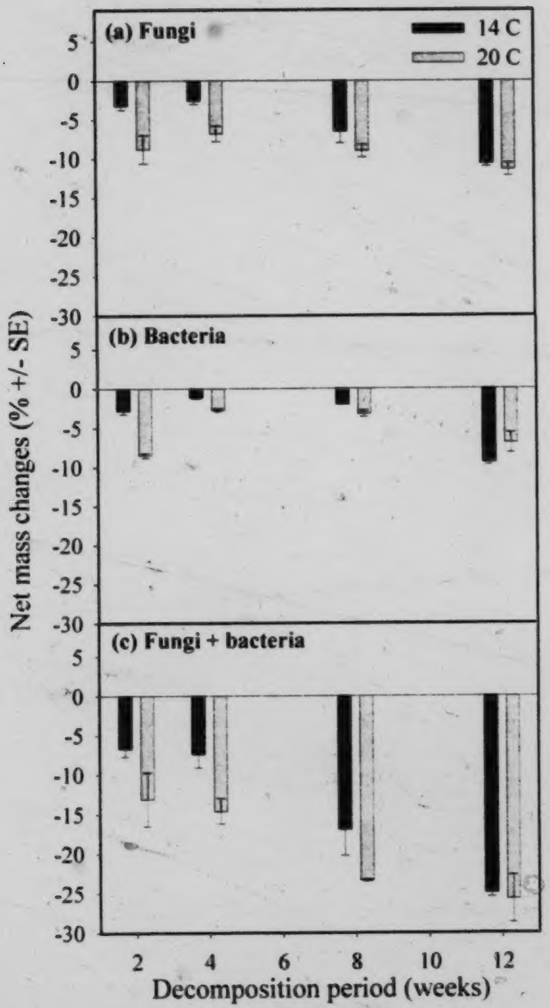

Figure 5-1. Mean *in vitro* net mass changes of *Carex aquatilis* rhizomes caused by (**a**) the three most common fungi (*Mucor hiemalis*, *Phialocephala dimorphospora*, and *Trichoderma harzianum*), (**b**) the three most common bacteria (*Arthrobacter* sp. 1, *Lactobacillus* sp., and *Leuconostoc* sp.), and (**c**) the three most common fungi and bacteria combined over a 12 week period.

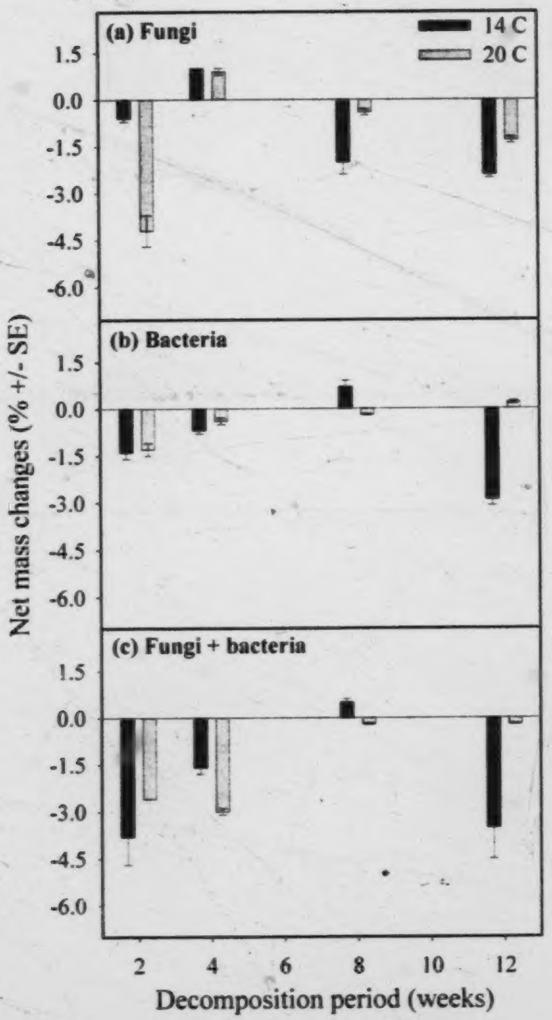

Figure 5-2. Mean *in vitro* net mass changes of *Sphagnum fuscum* plants caused by **(a)** the three most common fungi (*Mucor hiemalis*, *Penicillium thomii*, and *Trichoderma viride*), **(b)** the three most common bacteria (*Arthrobacter* sp. 3, *Bacillus* sp. 2, and *Brevibacterium* sp.), and **(c)** the three most common fungi and bacteria combined over a 12 week period. Positive values indicate mass gains.

Table 5-1. Selected morphological characteristics of bacteria isolated from *Carex aquatilis* rhizomes and leaves from a fen and *Sphagnum fuscum* from a bog in southern boreal Alberta, Canada.

Substrates	Bacteria	Sizes (µm)	Shapes	Colony colours
C. aquatilis rhizomes	*Arthrobacter* sp. 1	1.3 x 0.5	rods (some cocci), single	yellow-orange
	Lactobacillus sp.	2.0 x 0.8	rods, single	pale brown, shiny
	Leuconostoc sp.	1.5 x 0.4	rods, single	pale brown
C. aquatilis leaves	*Arthrobacter* sp. 2	1.2 x 0.5	rods (some cocci), single	hyaline-yellow
	Bacillus sp. 1	1.7 x 0.6	rods, single and in pairs	brown, shiny
	Micrococcus sp.	0.7 x 0.6	cocci, single	pale yellow
S. fuscum plants	*Arthrobacter* sp. 3	1.1 x 0.4	rods, single	creamy, shiny
	Bacillus sp. 2	1.5 x 0.3	rods, single	pale yellow
	Brevibacterium sp.	1.5 x 0.3	rods, single	brown-purple, purple crystals in colony

Note: All bacteria were gram-positive.

Table 5-2. Bacteria and fungi isolated from *Carex aquatilis* rhizomes and leaves from a fen and *Sphagnum fuscum* from a bog in southern boreal Alberta, Canada.

Substrates	Bacteria	Fungi
C. aquatilis rhizomes	*Arthrobacter* sp. 1	*Mucor hiemalis* Wehmer
	Lactobacillus sp.	*Phialocephala dimorphospora* Kendrick
	Leuconostoc sp.	*Trichoderma harzianum* Rifai
C. aquatilis leaves	*Arthrobacter* sp. 2	Basidiomycete sp. 3
	Bacillus sp. 1	*Monocillium constrictum* (Bourchier) W. Gams
	Micrococcus sp.	*Penicillium chrysogenum* Thom
S. fuscum plants	*Arthrobacter* sp. 3	*M. hiemalis*
	Bacillus sp. 2	*Penicillium thomii* Maire
	Brevibacterium sp.	*Trichoderma viride* Pers. *ex* Gray

Table 5-3. Mean mass losses of three litter types from two peatlands in southern boreal Alberta, Canada, after 12 weeks decomposition *in vitro* by bacterial, fungal, and bacterial plus fungal populations and *in situ*.

Litter types	Temperatures	Mass losses (% ± SE)			
		Three most common bacteria	Three most common fungi	Three most common bacteria + fungi	*In situ*
Sphagnum fuscum plants	14 °C	-3.2 (0.02) *a1*	-2.4 (0.06) *b1*	-3.5 (0.74) *a1*	-17.5
	20 °C	-0.2 (0.03) *a2*	-0.5 (0.04) *b2*	-0.2 (0.01) *a2*	
Carex aquatilis leaves	14 °C	3.2 (1.21) *a1*	0.4 (1.86) *b1*	-1.7 (0.12) *c1*	-11.2
	20 °C	-3.9 (0.98) *a2*	-12.3 (2.67) *b2*	-8.0 (1.30) *b2*	
C. aquatilis rhizomes	14 °C	-7.3 (0.76) *a1*	-6.2 (1.21) *a1*	-24.9 (0.53) *b1*	-36.2
	20 °C	-6.5 (0.69) *a1*	-11.4 (1.94) *b2*	-25.7 (3.01) *c1*	

Note: Positive values indicate mass gains of the decomposing litters. Different italic letters indicate significant differences among the treatments for each litter type at each temperature, while different italic numbers indicate significant differences among temperature treatments for each litter type. n = 18 each for bacterial and fungal mass losses and n = 3 for bacterial plus fungal mass losses. *In situ* mass losses were determined from Thormann et al. (2001).

Table 5-4. Growth rates (mm) after 10 days on peptone-broth agar and enzymatic abilities of the eight fungi used in the *in vitro* decomposition study to degrade various carbon sources.

Fungal taxa	Growth rates			Carbon substrata				
	14 °C	20 °C		Cellulose	Gelatin	Pectin	Starch	Tannic acid
Basidiomycete sp. 3	68	> 80	n. s.	---	+	---	---	---
Monocillium constrictum	10	13	n. s.	+	+	---	+	+
Mucor hiemalis	> 80	> 80	n. s.	---	+	+	---	---
Penicillium chrysogenum	21	36	*	+	+	+	+	---
Penicillium thomii	15	26	*	+	+	+	+	---
Phialocephala dimorphospora	7	20	*	+	+	---	---	+
Trichoderma harzianum	> 80	> 80	n. s.	+	+	+	+	---
Trichoderma viride	> 80	> 80	n. s.	+	+	+	+	---

Note: * $p < 0.01$, n. s. = not significant; "+" indicates the ability and "---" the inability to degrade the individual carbon sources. n = 3 per treatment.

CHAPTER 6. THE MYCORRHIZAL STATUS OF THE DOMINANT VEGETATION ALONG A PEATLAND GRADIENT IN SOUTHERN BOREAL ALBERTA, CANADA [2]

INTRODUCTION

Peatlands have been defined as ecosystems where organic material accumulates to a depth greater than 40 cm and the water table is at or near the soil surface (Gorham 1991). Peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and 18% of Alberta's land surface (Vitt et al. 1996). In Alberta, fens and bogs cover approximately 11.4% and 4.9% of the land surface, respectively, while marshes are less common, covering only 1.5% of the land surface (Vitt et al. 1996). Bogs are ombrotrophic peatlands that receive nutrients only from precipitation and, in Alberta, are dominated by *Sphagnum* spp., *Picea mariana* (Mill.) BSP., and members of the Ericaceae. Conversely, fens are minerotrophic ecosystems that receive nutrients from ground- and surface-water flow as well as from precipitation. Fens can be subdivided into poor, moderate-rich, and extreme-rich fens, a classification based on water chemistry and characterized by the number of indicator moss species (Du Rietz 1949), whereby poor fens have few and extreme-rich fens have many moss species indicative of alkaline conditions. In Alberta, peatlands are dominated by *Sphagnum* species at the poor end and by "brown" mosses, such as *Drepanocladus aduncus* (Hedw.) Warnst., *Scorpidium scorpioides* (Hedw.) Limpr., and *Aulacomnium palustre* (Hedw.) Schwaegr., at the rich end of the gradient. Additionally, many shrub and herb species are found in fens. Marshes are minerotrophic ecosystems dominated by sedges, grasses, and reeds, generally have higher surface-water nutrients than fens, and are often associated with open bodies of water. Mosses, shrubs, and trees are generally absent due to high and fluctuating water levels. Marshes in southern boreal Alberta have peat substrates (Thormann and Bayley 1997) and were classified as peatlands in this study.

Mycorrhizas are mostly mutualistic associations between fungi and the roots of higher plants, in which the fungi form consistently recognizable and physically distinct associations without causing any perceivable negative effect (Fernando 1995). There are five common types of mycorrhizas: ectomycorrhizas, vesicular-arbuscular mycorrhizas (VAM), arbutoid mycorrhizas (ectendomycorrhizas), ericoid mycorrhizas, and orchid mycorrhizas. Read (1991) and Smith and Read (1997) provide detailed information on these different types of mycorrhizas.

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[2] A version of this chapter has been published: Thormann, M. N., R. S. Currah, and S. E. Bayley. 1999. The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta, Canada. Wetlands **19**: 438-450.

Briefly, ectomycorrhizal fungi are characterized by root-tip hypertrophy (excessive growth), the formation of a Hartig net (intercellular mycelium enveloping the cells of the cortex and epidermis of the plant root), and a mantle (a compact layer of mycelium enveloping the root tips of the host plant). These fungi synthesize a wide range of enzymes, such as cellulases (Linkins and Antibus 1982), phosphatases (Alexander and Hardy 1981), and polyphenol-oxidases (Giltrap 1982), that enable them to degrade litter. The ability of ectomycorrhizal fungi to mobilize nitrogen from proteins (Abuzinadah and Read 1986) may be their most important role. Many of these nutrients, as well as water, are translocated through the mycelium of the ectomycorrhizal fungus to the host plant in exchange for photosynthates (Smith and Read 1997).

Vesicular-arbuscular mycorrhizal fungi manifest themselves as highly branched arbuscules and swollen vesicles (structures involved in the exchange and storage of nutrients) in root cortical cells. VA-mycorrhizal fungi have a more restricted range of abilities to access and mobilize nutrients (Read 1991). However, increased access to phosphates via the proliferation of their mycelia throughout the soil horizons (Sanders and Tinker 1971) and the synthesis of alkaline phosphatases (Gianinazzi-Pearson and Gianinazzi 1983), which solubilize bound phosphates (Owusu-Bennoah and Wild 1980), provide host plants with additional P for growth.

Arbutoid mycorrhizal fungi are characterized by the formation of a mantle, a Hartig net, and intracellular proliferations within cortical cells of their host plants, primarily achlorophyllous Monotropaceae (Smith and Read 1997). Translocation of nitrogen (N), phosphorus (P), and carbon (C) by arbutoid mycorrhizal fungi from woody plant species to the members of the Monotropaceae has been shown in field studies, a process termed 'myco-heterotrophy' by Leake (1994).

Ericoid mycorrhizas are characterized by septate hyphae forming successive coils within root cortical and/or epidermal cells (Stoyke and Currah 1991). It is thought that the primary advantage to ericaceous host plants is access to otherwise unavailable nitrogen pools (Read 1991). Ericoid mycorrhizal fungi can access ammonium ions and use amino acids from organic soil horizons via the action of enzymes, such as proteases and acid phosphatases (Pearson and Read 1975). In addition, although the mycelium of ericoid mycorrhizal fungi does not extend far beyond the cortical cells of the host plants into the surrounding soil, it has the ability to degrade a number of complex organic substances (tannins, lignin, chitin) (Leake 1987, Leake and Read 1989, Haselwandter et al. 1990) and thereby mobilize some of the generally limiting nutrients.

Orchid mycorrhizas form pelotons (coiled, anastomosed hyphae) within orchid roots (Zelmer et al. 1996), and experimental evidence suggests that these endophytes are involved in the uptake of nutrients from the soil solution, including C and P (Alexander et al. 1984). It has been shown that germinating orchid seeds *in situ* require the presence of the mycorrhizal fungus to survive, although the seeds of many orchid species can also be grown to maturity *in vitro* without a mycorrhizal fungus (Smith and Read 1997).

Mycorrhizas are common in many habitats, and their presence suggests that they play ecologically significant roles (Wetzel and van der Valk 1996, Näsholm et al. 1998, van der Heijden et al. 1998), such as the acquisition, storage, and translocation of nutrients. The significance of mycorrhizas has been shown in many studies, particularly in stressed ecosystems, including high altitude (Haselwandter and Read 1982), high latitude (Kohn and Stasovski 1990), and nutrient-limited ecosystems (Haselwandter 1987). Host plants frequently have elevated tissue concentrations of N and P, show reduced wilting due to water stress (Harley and Smith 1983) or high salinity (Rozema et al. 1986), and have higher water-uptake rates than non-infected plants (Harley and Smith 1983). Most of the hypothesized functions of mycorrhizal fungi have resulted from *in vitro* studies; however, recent *in situ* studies indicate that mycorrhizal fungi indeed are able to access otherwise unavailable nutrient pools and translocate these nutrients to host plants (Näsholm et al. 1998).

Information on mycorrhizas in peatlands is limited and often contradictory (Wetzel and van der Valk 1996). The absence of VAM in aquatic macrophytes of the Cyperaceae and Juncaceae has been reported by many researchers (Harley and Smith 1983, Anderson et al. 1984, Allen 1991) and is possibly due to fine roots that enable these plants to efficiently absorb nutrients from the rhizosphere (Powell 1975). Conversely, Reid et al. (1976) and Wetzel and van der Valk (1996) reported the presence of VAM in temperate and prairie pothole ecosystem vegetation (members of the Cyperaceae and Juncaceae), respectively. Similar reports were made for halophytic wetland species (Ho 1987) and aquatic plants, such as species in the genera *Littorella*, *Lobelia*, and *Isoetes* (Søndergaard and Laegaard 1977). Generally, mycorrhizas were noted in moist-to-wet habitats with no "functional" mycorrhizas being present (*i.e.*, arbuscules were absent) in the wettest habitats along a soil moisture gradient (Anderson et al. 1984, Lodge 1989). Thus, waterlogged soils may inhibit the formation of mycorrhizas. Furthermore, some plant species, most notably *Salix* spp. and *Populus* spp., can form both ecto- and VA-mycorrhizas simultaneously or in succession on the same root system (Newman and Reddell 1987). However, causes and mechanisms of the mycorrhizal succession on the same root system remain uncertain.

The scarcity of data on the mycorrhizal status of peatland plants warrants further investigation. Many plant species have not been examined for mycorrhizas, although their mycorrhizal status may have been inferred due to the presence of nearby fruiting bodies of known mycorrhizal fungi. The most comprehensive survey of the mycorrhizal status of plants in Alberta concentrated on parkland, prairie, and alpine plant species, largely excluding peatland ecosystems (Currah and Van Dyk 1986). In light of the importance of wetlands (National Wetlands Working Group 1988) and their significant contribution to Alberta's landscape (Vitt et al. 1996), I conducted a survey on the occurrence of mycorrhizal fungi in the dominant vegetation in wetlands. My objectives were to provide the first comprehensive survey of the mycorrhizal status of the vascular vegetation in southern boreal bogs, fens, and marshes in Alberta. These types of peatlands vary greatly in their pH, water levels, water-level fluctuations, surface-water nutrient concentrations, and peat thicknesses (Szumigalski and Bayley 1997, Thormann and Bayley 1997). Furthermore, the ecological significance of the occurrences of mycorrhizal fungi associated with the dominant vegetation in peatlands was addressed.

I hypothesized that (1) all plant species examined in bogs and fens will be mycorrhizal because closely related species from non-peatland ecosystems have previously been shown to be mycorrhizal, (2) the ectomycorrhizal fungus *Cenococcum geophilum* Fr. will be present in roots of all woody plant species due to its circumboreal distribution (LoBuglio et al. 1992), and (3) the dominant vegetation of marshes will be non-mycorrhizal, because both VAM and ectomycorrhizal fungi decrease in occurrence in waterlogged soils (Anderson et al. 1984, Lodge 1989).

METHODS

Study area and site descriptions

The vascular plant species were collected from ten peatlands that represent the range of peatlands present in southern boreal Alberta, Canada: two bogs (Bleak Lake bog, Perryvale bog), one poor fen, four moderate-rich fens (wooded fen, riverine sedge fen, lacustrine sedge fen, floating sedge fen), one extreme-rich fen, and two marshes (riverine marsh, lacustrine marsh). These peatlands represent a gradient based on the elevation of the surface water, inflow of nutrients, nutrient concentrations, pH (Thormann and Bayley 1997), vegetation type, and peat-accumulation potentials (Mitsch and Gosselink 1993). Mild summers and cold, snowy winters characterize the climate of southern boreal Alberta. The mean annual temperature is 1.7 °C, and the total mean precipitation is approximately 500 mm for the ten sites (Environment Canada

1982). These peatlands lie within the Subhumid Low Boreal ecoclimate region of Canada (Ecoregions Working Group 1989).

Physical and surface-water chemistry variables, locations, and dominant plant species are listed in Tables 6-1 and 6-2. More detailed site descriptions with respect to vegetation composition, aboveground plant production, and surface water chemistry are in Szumigalski and Bayley (1997) and Thormann and Bayley (1997). Vascular plant nomenclature follows Packer (1983) with the exceptions of *Petasites frigidus* var. *sagittatus*, which is in accordance with Cherniawsky and Bayer (1998), and *Carex utriculata*, which is in accordance with Griffiths (1989). *Sphagnum* and brown moss nomenclatures follow Anderson (1990) and Anderson et al. (1990), respectively.

Plant collection and determination of the mycorrhizal status

Four plants of each of the dominant plant species (Table 6-3) were carefully extracted in their entirety from the organic soil substrate within each peatland in mid-July 1997. Some plant species, such as *Picea mariana*, *Carex lasiocarpa*, and *Larix laricina*, were collected from several peatlands to ascertain if their mycorrhizal status changed along this gradient (Table 6-3). The plants were wrapped in plastic bags, placed in a cooler for transportation, and stored in a refrigerator at 4 °C until they were processed (within three days after collection). Four well-developed rootlets (primary root with secondary roots and adventitious root hairs [in members of the Ericaceae] attached) clearly connected to the root axis were removed from each plant. Rootlets were washed in distilled water (d-H_2O) and stored in 37% formaldehyde until further processing.

Methods for clearing and staining of root samples followed Brundrett et al. (1994). A random sub-set of rootlets from each plant species was cleared with a 10% KOH solution in an autoclave for 15 minutes at 121 °C (liquid cycle). Darkly pigmented roots of most woody plant species were autoclaved for 25 minutes at 121 °C (liquid cycle) to ensure optimal clearing of the rootlets. Cleared rootlets were thoroughly washed with d-H_2O and then stained with 0.1% chlorazol black E in equal parts water, glycerine, and 80% lactic acid in an autoclave for 15 minutes at 121 °C (liquid cycle). This process did not result in excessive damage to the rootlets and allowed for the examination of root cortical cells under a light microscope. The stained roots were washed with d-H_2O and stored in 50% glycerine in a glass vial with a tight seal until further processing.

Random subsets of the cleared and stained rootlets were mounted on slides (ten 1-cm pieces of each rootlet), squashed, and scanned for the presence of mycorrhizas (at 400x magnification) according to the characterization of Malloch and Malloch (1981). Briefly, root-tip hypertrophy, the presence of a Hartig net, and a mantle characterized ectomycorrhizas, while highly branched arbuscules and vesicles indicated the presence of VAM fungi. The absence of vesicles and the presence of arbuscules was deemed sufficient proof for the presence of VAMs because arbuscules are so far only known to be formed by VA-mycorrhizal fungi; however, the presence of vesicles but not arbuscules was insufficient to ascertain the occurrence of VAM fungi. Ericoid mycorrhizas were judged to be present if septate hyphae formed successive hyphal coils within root cortical cells (Stoyke and Currah 1991). In addition, other hyphae or hyphal characters, such as septation (partitioning in hyphae), color, and clamp connections, and aggregations, such as sclerotia (masses of closely packed hyphae, often intracellular) and sclerotial plaques (extracellular sclerotia), were noted. No attempt was made to quantify the fungal infection or identify the fungi involved in these associations.

Morphological characterization of common ectomycorrhizas of *Salix planifolia*

The roots of *Salix planifolia* from the riverine sedge fen, a common shrub of fens in boreal Alberta (Packer 1983), were examined for ectomycorrhizas. Identification of the most frequently occurring ectomycorrhizas of this shrub followed Kernaghan and Currah (1998). Briefly, *S. planifolia* roots were carefully extracted from the soil in mid-May 1997, stored on ice during transportation, and refrigerated until further processing (within one week after collection). Representative rootlets were carefully washed with d-H_2O, examined under a dissecting microscope, and the morphology of the ectomycorrhizal system (branching patterns, tip shapes and dimensions, colors, textures, and lustres), mycelial strands (attachments, frequencies, colors, surface descriptions), emanating hyphae (frequency and shape), and mantle anatomy (outer and inner layers, presence or absence of specialized cells, chemical reactions) were described according to Agerer (1987-1995).

RESULTS AND DISCUSSION

Ericoid mycorrhizal plant species

All ericaceous plant species (members of the Ericaceae) in all fens and bogs were ericoid mycorrhizal (Table 6-3). The mycorrhizal status of members of this family has been demonstrated numerous times in the past (Malloch and Malloch 1982, Bledsoe et al. 1990, Stoyke and Currah 1991, Treu et al. 1996, Hambleton and Currah 1997). Although these studies were conducted in a variety of habitats (alpine, arctic, boreal, parkland), the results are remarkably consistent for members of this family and also apply to ericaceous plants in peatlands. However, some members of the Ericaceae, such as *Rhododendron*, may be ectomycorrhizal (Mueller et al. 1986), and considering the close relationship of *Ledum* with *Rhododendron* (Kron and Judd 1990), it is possible to expect the occurrence of ectomycorrhizas in *Ledum* as well.

Oidiodendron maius Barron and *Hymenoscyphus ericae* (Read) Korf & Kernan with its anamorph (asexual state), *Scytalidium vaccinii* Dalpé, Litten & Sigler, have been isolated from roots of ericaceous plants in temperate and alpine habitats and are considered to be major mycobionts (Read 1983, Read 1991, Hambleton and Currah 1997). Although some ericaceous plant species may be ectomycorrhizal (Mueller et al. 1986), I did not observe clamped hyphae among cortical cells in any of my samples. Ericaceous plant species generally grow in habitats, such as peatlands, limited by available nutrients, low temperatures, and/or short growing periods (Grime 1979). Peatland soils are generally not nutrient-poor; however, the total quantities of available nutrients are low because they are bound to organic substrates and are thus unavailable to plants for growth (Mitsch and Gosselink 1993).

Many metal ions, such as aluminum, become mobile at low pH and can lead to growth-inhibiting or lethal conditions for plants (Salisbury and Ross 1985). Ericoid mycorrhizal fungi can regulate the uptake of metal ions into the roots of their host plants, thereby averting potential metal toxicities (Read 1991). Furthermore, organic acids can be metabolized and used as carbon sources (Read 1991). Although neither organic acid nor surface-water concentrations of metals were measured in this study, four of the ten peatlands (Bleak Lake and Perryvale bogs, poor fen, and wooded fen) are characterized by a pH lower than 6.1 (Table 6-1). Therefore, plant species in these four peatlands may be exposed to high concentrations of organic acids and soluble metal ions. These four peatlands have a diverse understory of ericaceous plant species that contribute substantially to the overall production of these sites (Szumigalski and Bayley 1997, Thormann and Bayley 1997). Thus, the presence of ericaceous plant species in these peatlands may not be attributable to their superior competitive abilities but rather to their mycorrhizal association that permits them to tolerate stresses (Read 1991, Hambleton and Currah 1997).

Ectomycorrhizal plant species

All woody, non-ericaceous plant species in all fens and bogs were ectomycorrhizal (Table 6-3). The cosmopolitan ectomycorrhizal fungus *Cenococcum geophilum* was found on most roots of *Picea mariana* in bogs and fens, as well as on *Larix laricina*, *Salix pedicellaris*, and *Salix planifolia* in poor, moderate-rich, and extreme-rich fens (Table 6-3). These results suggest that this fungus is not adversely affected by surface-water nutrient concentrations, pH, or water levels.

The ectomycorrhizal status of *P. mariana* and *L. laricina* has been demonstrated previously in north-western Ontario boreal forests (Malloch and Malloch 1981), and *Betula pumila* was determined to be ectomycorrhizal in arctic (Kohn and Stasovski 1990) and boreal ecosystems (Malloch and Malloch 1981). Although *Salix planifolia*, *Salix pedicellaris*, and *Salix candida* have not been examined in previous studies, other *Salix* species from arctic (Bledsoe et al. 1990, Kohn and Stasovski 1990, Treu et al. 1996), alpine (Haselwandter and Read 1982, Dhillion 1994), and boreal forest (Malloch and Malloch 1981, Currah and Van Dyk 1986) ecosystems were ectomycorrhizal as well.

Salix planifolia, *Salix pedicellaris* (from the poor and moderate-rich fens), and *Betula pumila* var. *glandulifera* (from the moderate-rich fens) of this study were simultaneously ecto- and VA-mycorrhizal (Table 6-3). The "bi-mycorrhizal" status of *Salix* and *Betula* species is not uncommon and has been reported previously from alpine (Dhillion 1994) and boreal (Malloch and Malloch 1981) habitats. This phenomenon depends partly on plant age, and succession from one to the other may be due to antagonistic relationships between the two mycorrhizal types, changes in host physiology, soil biota, or the microenvironment (Last et al. 1983, Lapeyrie and Chilvers 1985).

All woody plant species in all bogs and fens were ectomycorrhizal (Table 6-3), supporting the premise that ectomycorrhizal fungi prefer moist but well-drained soils (Lodge 1989) of high organic content with low N and P availabilities (Smith and Read 1997) and low pH (Abuzinadah and Read 1986). Waterlogged soils, characteristic of peatlands, inhibit oxygen absorption by shrub and tree roots (Reader 1978) and generally inhibit the formation of ectomycorrhizas due to low dissolved oxygen concentrations (Lodge 1989). However, shrubs and trees in these fens and bogs grow primarily on drier hummocks rather than in wet hollows (Thormann and Bayley 1997) and were ectomycorrhizal (Table 6-3). The presence of some ectomycorrhizal fungi, such as *Cenococcum geophilum*, may also be attributed to their cosmopolitan nature.

Salix planifolia roots from the riverine sedge fen were associated with the ectomycorrhizal fungus *Cenococcum geophilum* as well as with fungi resembling species in *Laccaria* and *Tomentella*. *Cenococcum geophilum* mycorrhizas were characterized by a stellate pattern of the hyphae on the mantle surface, thick walled mantle hyphae, and dark brown to black, unclamped emanating hyphae. The inner and outer mantle layers consisted of net synenchyma tissues. The *Tomentella*-like association was characterized by a monopodially pinnate, straight-tipped ramification; emanating hyphae were rare, thick-walled, straight, and darkly colored, and the mantle was thin and consisted of inner and outer pseudoparenchymatous tissues. The *Laccaria*-like ectomycorrhiza had a monopodially pinnate, straight-tipped ramification and outer net prosenchyma and inner net synenchyma mantle tissues.

In addition, fruiting bodies of *Cortinarius* sp., *Lactarius* sp., and *Russula fragilis* (Pers. *ex* Fr.) Fr. were collected late in the growing season; these taxa are known to form ectomycorrhizas with woody plant species (Kernaghan and Currah 1998). Identification of ectomycorrhizal fungi was limited to the most frequent ones associated with the dominant willow species in the riverine sedge fen. Those that were identified are not specific to *Salix* but have also been identified previously from *Picea*, *Abies*, and other trees and shrubs (Kernaghan and Currah 1998).

VAM plant species

None of the dominant herbaceous plant species along this peatland gradient was VA-mycorrhizal (Table 6-3). The degree of VAM fungal colonization of plants is negatively affected by calcium, magnesium (Anderson et al. 1984), phosphorus, pH (Anderson et al. 1984, Wetzel and van der Valk 1996), and water levels (Lodge 1989). The host plant species may also determine the degree of colonization by VAM fungi (Wetzel and van der Valk 1996).

It is possible that the surface water concentrations of calcium and phosphorus and the pH (Table 6-1) are too high to facilitate the formation of VA-mycorrhizas in these two marshes (Table 6-3). Wetzel and van der Valk (1996) reported the consistent occurrence of VA-mycorrhizal fungi in all of their wetland vegetation samples from Iowa and North Dakota. In contrast to their wetlands, my marshes generally had a higher pH (mean of 7.4) and higher surface water concentrations of nitrate (mean of 16 $\mu g\ L^{-1}$) and phosphorus (soluble reactive phosphorus, mean of 89 $\mu g\ L^{-1}$) (Table 6-1), potentially inhibiting the formation of VA-mycorrhizas in my marsh taxa (Table 6-3). Additionally, poorly drained soils generally inhibit the formation of VA-mycorrhizas (Lodge 1989) due to low availability of oxygen (Saif 1981).

The peat horizon in the lacustrine marsh was anoxic due to frequent high water levels (Thormann and Bayley 1997), also possibly inhibiting the growth of VA-mycorrhizal fungi. Although surface water concentrations of calcium (bogs: mean of 3 mg L^{-1}; fens: mean of 26 mg L^{-1}), nitrate (bogs: mean of 9 μg L^{-1}; fens: mean of 8 μg L^{-1}), and SRP (bogs: mean of 11 μg L^{-1}; fens: mean of 26 μg L^{-1}), as well as the pH (bogs: mean of 3.9; fens: mean of 6.6) were substantially lower in these fens and bogs (Table 6-1), typical VA-mycorrhizal plant taxa, such as members of the Poaceae, Labiatae, and Asteraceae (Newman and Reddell 1987), generally do not form significant components of these peatland vegetation strata (Thormann and Bayley 1997).

Non-mycorrhizal plant species

Although *Calamagrostis canadensis* (riverine marsh) and *Rubus chamaemorus* L. (Bleak Lake bog) had vesicles indicative of VAM fungi (Table 6-3, Figure 6-1e), they could not be classified as VA-mycorrhizal because arbuscules were absent. The VAM status of the grass *C. canadensis* has been reported previously by Malloch and Malloch (1982), Anderson et al. (1984), and Wetzel and van der Valk (1996) from north-eastern Ontario, Illinois, and Iowa, respectively. Although arbuscules were observed in root cortical cells by Anderson et al. (1984), they were absent in my samples, and the occurrence of vesicles was low. Compared to the Iowa wet meadows of Wetzel and van der Valk (1996), the riverine marsh had higher concentrations of nitrate and phosphorus, higher pH, and higher mean growing season water levels (Table 6-1), which may have reduced infection levels and suppressed the formation of arbuscules within root cells of *C. canadensis* (Table 6-3).

Rubus chamaemorus (Bleak Lake bog) also had vesicles indicative of VAM fungi but was considered to be non-mycorrhizal because of the absence of arbuscules (Table 6-3). Malloch and Malloch (1982) previously reported that *Rubus* spp. in northwestern boreal Ontario were non-mycorrhizal; however, they suspected that this genus may be VA-mycorrhizal. In support, Currah and Van Dyk (1986) reported the presence of VA-mycorrhizal fungi in *Rubus* spp. roots from parkland ecosystems in Alberta.

I collected my plant samples in mid-July, and it is possible that arbuscules decrease and vesicles increase in frequency in wetland plant roots from early spring to summer and fall due to the reported seasonality of VA-mycorrhizal formation in many plant species and ecosystems (Brundrett 1991). Seasonal changes in VA-mycorrhizal formations are regulated by root phenology and are at their maximum during new root growth (Brundrett and Kendrick 1990), which may have preceded my collection time.

Most members of the Cyperaceae, Typhaceae, Equisetaceae, Droseraceae, Gentianaceae, Asteraceae, and Liliaceae were non-mycorrhizal (Table 6-3). Previously reported results regarding the mycorrhizal status of members of these families are variable.

Carex species have received a significant amount of attention with respect to their mycorrhizal status in alpine, arctic, boreal, and grassland ecosystems in North America (Malloch and Malloch 1982, Anderson et al. 1984, Bledsoe et al. 1989, Kohn and Stasovski 1990, Rickerl et al. 1994, Treu et al. 1996, Wetzel and van der Valk 1996, Miller et al. in press) and Europe (Søndergaard and Laegaard 1977, Haselwandter and Read 1980, Haselwandter and Read 1982, Blaschke 1991). The results of these studies are contradictory, as some report *Carex* as non-mycorrhizal, while others describe the presence of VAM. In most studies, the VA-mycorrhizal status of *Carex* species is based on the presence of vesicles and rarely on arbuscules. The presence of arbuscules was used previously as a definition indicating the presence of VAM fungi in plant roots (Malloch and Malloch 1981, 1982); however, the occurrence of vesicles alone has since been accepted as sufficient evidence for the presence of VAM fungi (Wetzel and van der Valk 1996). Although I found some vesicles in cortical cells of the roots of my *Carex* species, I did not find arbuscules and therefore classified the *Carex* species in these fens and marshes as non-mycorrhizal. Since some non-VAM fungi, such as *Rhizoctonia*, some members of the Chytridiomycota, and Pythiaceous fungi (Alexopoulos et al. 1996), also produce vesicle-like structures in plant roots, differentiation between those and vesicles of VAM fungi can be problematic and lead to misidentifications. Thus, the presence of arbuscules was a requirement for acceptance of the VAM status in this study.

A study of three *Typha* species in a Minnesota marsh (Stenlund and Charvat 1994) demonstrated that up to 40% of roots were colonized by VAM fungi, while a similar study of *Typha* X *glauca* Godr. in South Dakota (Rickerl et al. 1994) reported no vesicles. My results of the mycorrhizal status of *Typha* concur with the latter study. *Smilacina trifolia* (L.) Desf. (Liliaceae) was previously reported to have vesicles, arbuscules, and coils in its roots (Currah and Van Dyk 1986); these results are contradictory to those reported here. Currah and Van Dyk's (1986) reports of the non-mycorrhizal status of *Menyanthes trifoliata* L. (Gentianaceae) and *Equisetum fluviatile* (Equisetaceae) are in agreement with mine (Table 6-3). The only dominant plant species of the Asteraceae in these peatlands was *Petasites frigidus* var. *sagittatus* Cherniawsky and Bayer in the wooded fen. I found no structures indicative of mycorrhizal fungi in its roots (Table 6-3); however, Malloch and Malloch (1982) and Currah and Van Dyk (1986) both reported *Petasites* to be VA-mycorrhizal in boreal and parkland ecosystems. *Drosera* *rotundifolia* (Droseraceae) had not been previously examined for the presence of mycorrhizal fungi and is shown to be non-mycorrhizal in my study (Table 6-3), possibly due to the insectivorous mode of nutrient acquisition of this plant genus (Packer 1983).

Mycelium radicis atrovirens

In addition to the aforementioned typical structures formed by ericoid, ectomycorrhizal, and VA-mycorrhizal fungi, a diverse assemblage of hyphae was found in and on the roots of most of the examined root samples (Table 6-3). These hyphae were dematiaceous (darkly pigmented), hyaline (Figures 6-1a, 6-1d), septate (Figure 6-1a), aseptate (Figure 6-1e), with and without clamp connections, some of them forming microsclerotia (Figure 6-1g) and others sclerotial plaques enveloping small (Figure 6-1b) or large (Figure 6-1d) portions of the roots. Several extracellular hyphae terminated in appressoria (swollen hyphal structures used for attachment in the early stages of infection) on root surfaces (Figure 6-1f), while others grew intracellularly (Figure 6-1c). None of the fungi forming these hyphae was identified.

Sterile, darkly pigmented hyphae were first mentioned by Melin (1922) who designated them *Mycelium radicis atrovirens* (MRA). These fungi are commonly observed in herbaceous (Currah et al. 1987, Stoyke and Currah 1991) and woody (Summerbell 1987, Danielson and Visser 1990, Hennon et al. 1990) plants in temperate, alpine, and arctic habitats. Recent studies designated some species of the genera *Leptodontidium*, *Phialocephala*, and *Phialophora* as MRA (Currah et al. 1988, Currah and Tsuneda 1993, Fernando and Currah 1995); however, their ecological significance remains uncertain (Jumpponen and Trappe 1998).

Melin (1922) referred to an association formed by MRA fungi on roots of alpine tree species as "pseudomycorrhizas", a term later adopted by Wang and Wilcox (1985) to describe weakly pathogenic fungi that formed ectomycorrhiza-like associations with host plants. However, Danielson and Visser (1990) consider MRA to be mycorrhizal and Haselwandter and Read (1982) showed that some isolates of MRA increased shoot P levels and shoot and root dry weights of *Carex* spp. from alpine habitats. The authors, however, caution against extrapolations of their results. Stoyke and Currah (1991) suggested that MRA fungi may predominate in plant species in high altitude ecosystems, although I have found them in southern boreal peatlands as well (Table 6-3). Other studies have reported their pathogenic effects on host plants (Livingston and Blaschke 1984, Summerbell and Malloch 1988).

Sclerotial plaques (Figure 6-1d) and microsclerotia (Figure 6-1g) occurred on some plant species (Table 6-3) and have previously been described by Read and Haselwandter (1981) and

Treu et al. (1996) from Austria and Alaska, respectively. These sclerotial structures were formed by "dark, septate" fungi, which were ascribed to species of *Rhizoctonia* and *Phialophora* by Haselwandter (1987). Dark, septate fungi encompass a wide assemblage of different species or strains of fungi, and the literature does not always specify whether these fungi form sclerotia in or on roots (Treu et al. 1996). The ecological significance, if any, of these fungi is unclear (Jumpponen and Trappe 1998); however, they have been found in great abundance in highly stressed ecosystems, such as those of high altitudes and latitudes. It has been suggested that these fungi are mutualistic rather than parasitic (Treu et al. 1996). Treu et al. (1996) classified them as "mycorrhizas" although they warned that this term might be misleading and that a new category of mycorrhizas should be erected to encompass those forming with dark, septate fungi. Most reports of dark, septate fungi in roots of plants originate from studies of stressed ecosystems (Currah and Van Dyk 1986, Dhillion 1994, Treu et al. 1996), and it comes as no surprise that these fungi also occur frequently in peatlands. Some plant species, particularly members of the Cyperaceae, may be predisposed to be hosts of dark, septate fungi in their roots because these fungi may assume the role of VAM fungi in conditions where VAM fungi can no longer persist (Haselwandter and Read 1980), possibly due to the waterlogged, anoxic soil conditions.

Rhizoctonia

Rhizoctonia sp. has been identified in addition to a large number of other fungi with brown or tan hyphae. Several stained hyphae of this study resemble *Rhizoctonia* (Figure 6-1) and appeared in many different plant roots, most notably in members of the Cyperaceae and Typhaceae in fens and marshes (Table 6-3). Species of *Rhizoctonia* are characterized by a near right-angle hyphal branching pattern, the absence of clamp connections, and constrictions of hyphae near their points of origin (Alexopoulos et al. 1996). Their presence is not surprising, because *Rhizoctonia* and *Rhizoctonia*-like species have been encountered in apparently healthy roots in several previous studies (Haselwandter and Read 1980, Currah et al. 1987, Dhillion 1994).

It is possible that some species listed as non-mycorrhizal in my study may in fact be mycorrhizal. My conclusions might be different if collections were made during other times of the year, the quantity of root material examined larger, environmental conditions different, and/or the levels of proliferation of the mycorrhizal fungi in plant roots low and therefore not detected by my survey method. It is also possible that some of the previously examined plant species from other studies are mycorrhizal in non-peatland ecosystems, but that their mycorrhizal status changes in peatlands because of significantly different water and nutrient regimes.

CONCLUSIONS

The majority of the dominant plant species in southern boreal bogs and fens in Alberta are mycorrhizal, supporting hypothesis one. All ericaceous plant species in both fens and bogs showed coils of hyphae in root cortical cells, indicative of ericoid mycorrhizas. Members of the Pinaceae and Salicaceae formed ectomycorrhizas with *Cenococcum geophilum*, supporting hypothesis two. *Laccaria*-like and *Tomentella*-like ectomycorrhizal fungi were also identified on *Salix planifolia* roots in the riverine sedge fen. These two types of mycorrhizas are hypothesized to enhance N and P tissue concentrations of infected plant species, reduce water stress in dry habitats, and decrease metal toxicities at low pH among others, and these fungal associates most likely perform similar functions in nutrient-limited and acidic ecosystems, such as bogs and fens. VA-mycorrhizal fungi were not found in any of my herbaceous plant species in these fens and marshes.

Hypothesis three was also supported because members of the Cyperaceae, mostly *Carex* species, were non-mycorrhizal. However, sclerotial plaques, microsclerotia, clamped, unclamped, hyaline, and dematiaceous hyphae, some of which likely belong to the MRA complex of dematiaceous root endophytes, were found colonizing the surfaces and interiors of cortical cells. These hyphae were not considered indicative of mycorrhizas, although previous studies have indicated that MRA fungi may also lead to enhanced plant growth and tissue nutrient concentrations in some plant species.

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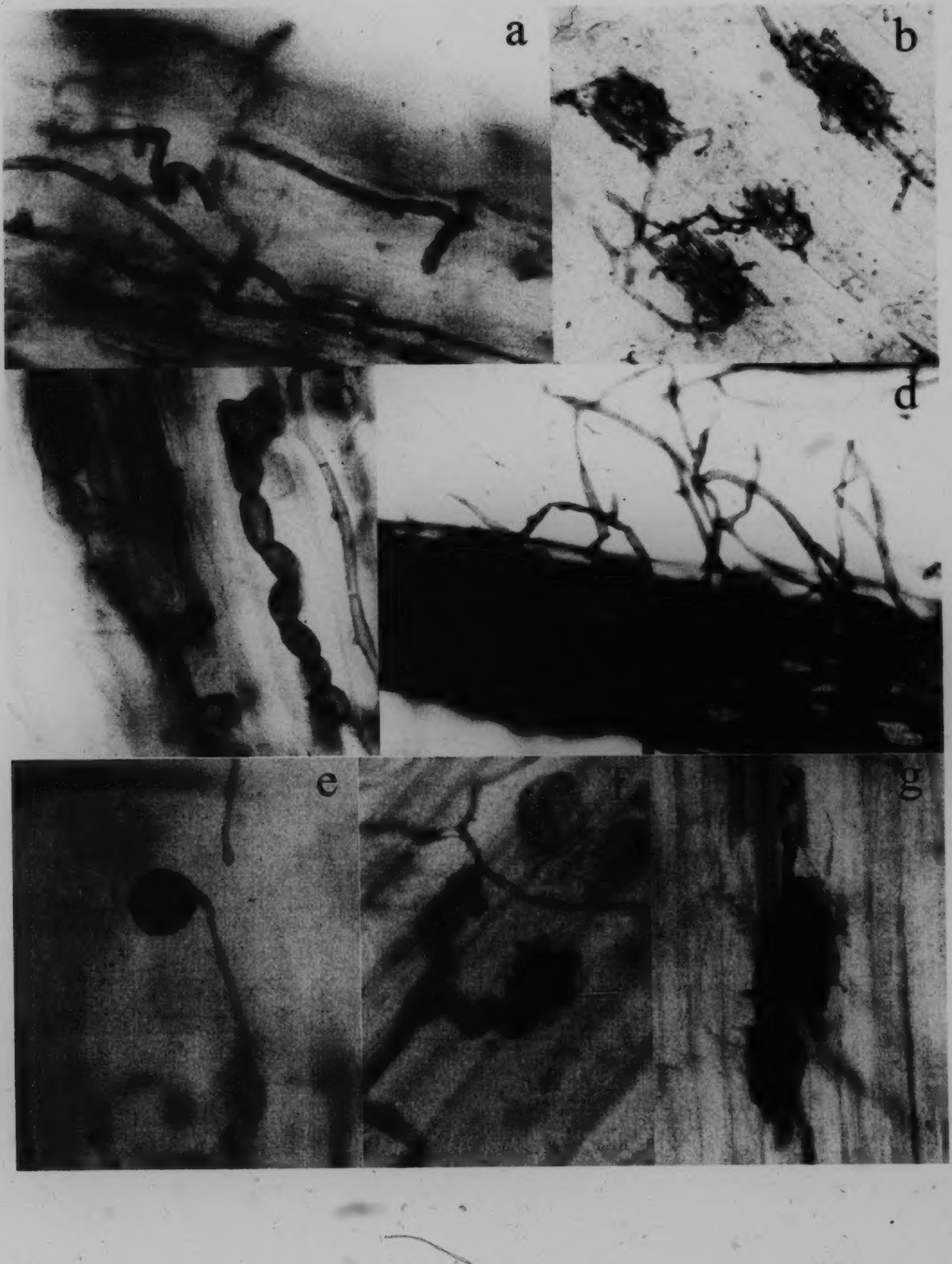
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Table 6-1. Physical and surface water chemical parameters (means and ranges) of ten peatlands in Alberta. SRP is soluble reactive phosphorus, conductivity is adjusted for pH and temperature (Szumigalski and Bayley 1997, Thormann and Bayley 1997).

Peatlands	Latitude/Longitude	Peat depth (m)	pH	Water level (cm)	Conductivity (µS cm^{-1})	NO_3^- (µg L^{-1})	NH_4^+ (µg L^{-1})	SRP (µg L^{-1})	Ca^{2+} (mg L^{-1})
Bleak Lake Bog	54° 41'N, 113° 28'W	5.0	3.9 (3.4 - 4.2)	-41.8 (-51.8 - -33.3)	0 ---	9 (3 - 24)	42 (12 - 108)	16 (1 - 63)	4 (2 - 6)
Perryvale Bog	54° 28'N, 113° 16'W	4.5	3.8 (3.7-3.9)	-34.0 (-22 - -41)	0 ---	8 (2 - 15)	10 (n.d. - 51)	5 (3 - 7)	2 (1 - 3)
Poor fen	54° 41'N, 113° 28'W	4.0	5.0 (4.3 - 5.2)	-24.0 (-34.2 - -11.6)	19 (15 - 27)	11 (2- 30)	21 (3 - 58)	72 (2 - 166)	8 (5 - 12)
Wooded fen	54° 28'N, 113° 17'W	4.5	6.1 (5.7 - 6.6)	-29.0 (-39.0 - -13.2)	26 (18 - 41)	9 (2 - 25)	19 (2 - 34)	24 (3 - 147)	12 (8 - 23)
Floating sedge fen	54° 28'N, 113° 17'W	1.0	6.2 (5.5 - 7.4)	-3.7 (-10.1 - -13.1)	75 (51 - 86)	7 (1 - 36)	36 (2 - 145)	9 (3 - 21)	9 (8 - 14)
Lacustrine sedge fen	54° 28'N, 113° 19'W	2.2	7.0 (6.2 - 7.8)	8.4 (-13.0 - 27.5)	197 (57 - 286)	6 (1 - 21)	32 (0.2 - 470)	4 (0.1 - 14)	21 (7 - 51)
Riverine sedge fen	54° 28'N, 113° 18'W	1.0	7.1 (6.3 - 8.1)	7.8 (-8.1 - 26.9)	231 (128 - 369)	8 (2 - 44)	17 (2 - 110)	21 (3 - 93)	18 (15 - 21)
Extreme-rich fen	53° 42'N, 113° 57'W	2.5	8.2 (7.8 - 8.4)	12.0 (5 - -34)	232 (195 - 259)	6 (3 - 10)	24 (1 - 79)	25 (2 - 112)	87 (58 - 115)
Riverine marsh	54° 28'N, 113° 23'W	0.8	7.4 (6.7 - 8.4)	10.6 (-14.7 - 50.2)	433 (293 - 717)	8 (2 - 20)	299 (2 - 2,275)	36 (2 - 114)	47 (30 - 64)
Lacustrine marsh	54° 10'N, 113° 34'W	1.6	7.4 (6.6 - 8.1)	0.4 (-33.0 - 40.1)	780 (651 - 1,186)	24 (3 - 233)	432 (4 - 3,516)	161 (9 - 867)	55 (43 - 66)

Table 6-2. The dominant vegetation of the ten peatlands in southern boreal Alberta, Canada.

Peatlands	Dominant vegetation
Bleak Lake Bog	*Picea mariana* (Mill.) BSP., *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Andromeda polifolia* L., *Sphagnum fuscum* (Schimp.) Klinggr.
Perryvale bog	*Picea mariana, Rhododendron groenlandicum, Andromeda polifolia, Sphagnum fuscum*
Poor fen	*Betula pumila* L. var. *glandulifera* Regel, *Salix pedicellaris* Pursh, *Carex* spp., *Sphagnum* spp.
Wooded fen	*Larix laricina* (Du Roi) K. Koch, *Betula pumila* var. *glandulifera*, *Carex* spp., *Tomenthypnum nitens* (Hedw.) Loeske
Lacustrine sedge fen	*Carex lasiocarpa* Ehrh., *Drepanocladus aduncus* (Hedw.) Warnst., *Aulacomnium palustre* (Hedw.) Schwaegr.
Riverine sedge fen	*Carex lasiocarpa, Carex aquatilis* Wahlenb., *Carex utriculata* Boott, *Equisetum fluviatile* L., *Salix planifolia* Pursh
Floating sedge fen	*Carex lasiocarpa, Carex rostrata* Stokes, *Salix pedicellaris, Andromeda polifolia*, *Sphagnum warnstorfii* Russ.
Extreme-rich fen	*Scirpus cespitosus, Drosera rotundifolia* L., *Scorpidium scorpioides* (Hedw.) Limpr., *Tomenthypnum nitens*
Riverine marsh	*Carex lasiocarpa, Carex aquatilis, Calamagrostis canadensis* (Michx.) Beauv., *Calamagrostis inexpansa* A. Gray
Lacustrine marsh	*Carex aquatilis, Carex utriculata, Typha latifolia* L., *Hippuris vulgaris* L.

Table 6-3. Mycorrhizal status of southern boreal peatland plant species in Alberta. Some plant species were sampled several times along the peatland gradient (bog - poor fen - moderate-rich fen - extreme-rich fen - marsh) in July 1997. EM = Ectomycorrhizas, VAM = vesicular-arbuscular mycorrhizas, NM = non-mycorrhizal.

Peatlands *	Plant species	Mycorrhizal status	Additional observations
Bogs	*Picea mariana* (Pinaceae)	EM	*Cenococcum geophilum*
	Chamaedaphne calyculata (Ericaceae)	Ericoid	dark, septate hyphae
	Andromeda polifolia (Ericaceae)	Ericoid	
	Rhododendron groenlandicum (Ericaceae)	Ericoid	dark, septate hyphae
	Oxycoccus quadripetalus (Ericaceae)	Ericoid	large quantities of hyphae on rootlets
	Vaccinium vitis-idaea (Ericaceae)	Ericoid	
	Eriophorum vaginatum (Cyperaceae)	NM	septate hyphae; microsclerotia
	Rubus chamaemorus (Rosaceae)	NM	vesicles
	Smilacina trifolia (Liliaceae)	NM	septate hyphae; clamped hyphae
Poor fen	*Larix laricina* (Pinaceae)	EM	
	Betula pumila var. *glandulifera* (Betulaceae)	EM	
	Salix pedicellaris (Salicaceae)	EM, VAM	*Cenococcum geophilum*
	Andromeda polifolia (Ericaceae)	Ericoid	large quantities of hyphae on rootlets
	Rhododendron groenlandicum (Ericaceae)	Ericoid	
	Oxycoccus quadripetalus (Ericaceae)	Ericoid	large quantities of hyphae on rootlets
	Carex lasiocarpa (Cyperaceae)	NM	septate hyphae; clamped hyphae; *Rhizoctonia*-like hyphae

	Menyanthes trifoliata (Gentianaceae)	NM	microsclerotia; septate hyphae; *Rhizoctonia*-like hyphae
	Smilacina trifolia (Liliaceae)	NM	hyaline, septate hyphae; clamped hyphae; microsclerotia
Moderate-rich fens	*Larix laricina* (Pinaceae)	EM	*Cenococcum geophilum*
	Picea mariana (Pinaceae)	EM	*Cenococcum geophilum*
	Betula pumila var. *glandulifera* (Betulaceae)	EM, VAM	large quantities of septate hyphae
	Salix pedicellaris (Salicaceae)	EM, VAM	*Cenococcum geophilum*
	Salix planifolia (Salicaceae)	EM, VAM	
	Andromeda polifolia (Ericaceae)	Ericoid	
	Oxycoccus quadripetalus (Ericaceae)	Ericoid	
	Petasites frigidus var. *sagittatus* (Asteraceae)	NM	microsclerotia; hyaline, septate hyphae
	Equisetum fluviatile (Equisetaceae)	NM	septate hyphae
	Carex aquatilis (Cyperaceae)	NM	septate hyphae; microsclerotia
	Carex lasiocarpa (Cyperaceae)	NM	microsclerotia; septate hyphae; *Rhizoctonia*-like hyphae; thick-walled hyphae
	Carex utriculata (Cyperaceae)	NM	vesicles
	Eriophorum vaginatum (Cyperaceae)	NM	hyaline, septate hyphae; *Rhizoctonia*-like hyphae; vesicles
Extreme-rich fen	*Larix laricina* (Pinaceae)	EM	*Cenococcum geophilum*
	*Picea mari*ana (Pinaceae)	EM	*Cenococcum geophilum*
	Salix candida (Salicaceae)	EM	
	Drosera rotundifolia (Droseraceae)	NM	
	Scirpus cespitosus (Cyperaceae)	NM	septate hyphae; clamped hyphae; hyaline, aseptate hyphae

Marshes	*Calamagrostis canadensis* (Poaceae)	NM	large quantities of hyphae on rootlets; vesicles
	Carex aquatilis (Cyperaceae)	NM	septate hyphae
	Carex lasiocarpa (Cyperaceae)	NM	dark, septate hyphae; clamped hyphae
	Carex rostrata (Cyperaceae)	NM	septate hyphae; small quantities of hyphae on rootlets
	Typha latifolia (Typhaceae)	NM	hyaline, septate hyphae; microsclerotia; dark, septate hyphae

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* The bogs include the Bleak Lake Bog and Perryvale Bog; the moderate-rich fens include the Wooded Fen, Floating Sedge Fen, Lacustrine Sedge Fen, and Riverine Sedge Fen; the mashes include the Riverine Marsh and Lacustrine Marsh. n = 4 per plant species per peatland type.

CHAPTER 7. CONCLUSIONS

Studies examining decomposition rates of belowground plant tissues in peatlands are scarce despite the significant contribution these tissues make to the total plant production. Therefore, I measured mass losses of *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots in a rich, sedge-dominated fen and *Sphagnum fuscum* plants in a forested bog over a two year period (Chapter 2). After two years, mass losses of *C. aquatilis* rhizomes (75%) were significantly higher than those of *C. aquatilis* leaves and *S. planifolia* leaves, which were similar to each other (54 and 48%, respectively). *Sphagnum fuscum* and *S. planifolia* root mass losses also were similar to each other (21 and 29%, respectively), but they were significantly lower than those of the other three litter types. Different tissue nutrient concentrations as well as alkalinity- and phosphorus-related surface water chemistry variables correlated significantly with mass losses of different litter types; however, they alone did not explain all of the mass loss trends. The majority of sedge peat and carbon in the fen originates from *C. aquatilis* leaves (188 and 86 g m^{-2}, respectively), with the remainder originating from *C. aquatilis* rhizomes (102 and 47 g m^{-2}, respectively) after the first two years of decomposition. Conversely, the majority of *S. planifolia* peat and carbon originates from its roots (33 and 16 g m^{-2}, respectively) and the remainder from its leaves (24 and 11 g m^{-2}, respectively) over the same period. After the first two years of decomposition, 150 g m^{-2} of peat and 71 g m^{-2} of carbon remained from the decomposing *S. fuscum* in the bog.

While investigating these mass losses, sub-samples of the decomposing plant litters were processed to isolate filamentous microfungi involved in the decomposition of these litters. Ninety-five fungal species were identified and/or described from the decomposing plant litters (Chapter 3). These were three ascomycetes, ten basidiomycetes, 12 zygomycetes, and 70 Fungi Imperfecti. The majority of these species represent new records from the five substrates (*Sphagnum fuscum* plants from a bog and *Salix planifolia* leaves and roots and *Carex aquatilis* leaves and rhizomes from a fen). Canonical correspondence analyses (CCA) of these fungi revealed substantially different fungal communities among different plant litters (Chapter 4), showing a clear separation of the mycota of the dominant bog and fen plant species. Distinct succession patterns of the mycota in two of the five litter types were observed (*Sphagnum fuscum*, *C. aquatilis* leaves), with the remaining three litter types showing no clear succession patterns. Litter quality variables (TC, TN, and TP tissue nutrient concentrations and TC:TN quotients) correlated most often with the observed fungal communities of these litter types, indicating that these variables had a greater impact on the individual fungal communities than either physical or surface water chemistry variables in these two peatlands.

Although fungal and bacterial biomass and production varies among ecosystems, both contribute to the decomposition of organic materials. However, the relative importance of fungi and bacteria to the decomposition of the dominant bog and fen plant species is unknown. Furthermore, the effect of global warming on microbial communities and their abilities to decompose plant materials under these conditions remains poorly understood. Therefore, I examined the rates of decomposition of *Carex aquatilis* leaves and rhizomes from a fen and *Sphagnum fuscum* plants from a bog by their three dominant indigenous fungi and bacteria at 14 and 20 °C over a 12-week period *in vitro* (Chapter 5). Mass losses of *S. fuscum* plants by all fungi, all bacteria, and all fungi plus bacteria were significantly greater at 14 °C than at 20 °C, whereas mass losses of the *C. aquatilis* leaves by fungi, bacteria, and fungi plus bacteria were significantly greater at 20 °C than at 14 °C. No clear temperature and microbial community trends were apparent for *C. aquatilis* rhizome mass losses. Interactions among fungi and bacteria caused significant increases in mass losses of *C. aquatilis* rhizomes at both temperature regimes; however, this was not the case for the *C. aquatilis* leaves and *S. fuscum* plant litter types, possibly due to initial litter quality differences. Responses of individual fungi and bacteria also varied. After 12 weeks, *Trichoderma viride* and *Penicillium thomii* (both 2.2% at 14 °C) and *Brevibacterium* sp. (4.5% at 14 °C) caused the greatest mass losses of the *S. fuscum* plant litter. *Phialocephala dimorphospora* (28.4% at 20 °C) and *Arthrobacter* sp. 1 (8.0% at 20 °C) were the most successful fungus and bacterium, respectively, decomposing *C. aquatilis* rhizome litter, while the *C. aquatilis* leaf litter was best decomposed by *Monocillium constrictum* (10.6% at 20 °C) and *Bacillus* sp. 1 (8.0% at 14 °C). These data indicate that different fungi and bacteria respond differently to changes in atmospheric temperatures. Therefore, rates of C mineralization by fungi and bacteria in the acrotelm of peatlands will likely vary among different peatland types and plant litters under a global warming scenario. Predictions that decomposition will increase in different peatland types are simplistic.

The decomposition of plant litters by microbial communities in any ecosystem results in the transformation of organic materials into inorganic nutrients, such as nitrate, ammonium, and phosphates. Despite the high organic matter content of some soils, especially those of peatlands, where low decomposition rates limit the transformation of organic matter into inorganic nutrients, plants may be stressed due to the lack of biologically available nutrients to them. Mycorrhizal fungi have access to these plant biologically available nutrients via their suite of enzymes, enabling these fungi to mobilize, absorb, and translocate them to their vascular plant hosts in exchange for carbohydrates. I investigated the mycorrhizal status of the dominant vascular plant species occurring in ten peatlands along a bog - fen - marsh gradient (Chapter 6). All members of the Ericaceae were ericoid mycorrhizal, and members of the Salicaceae and Pinaceae were ectomycorrhizal. Also, some members of the Salicaceae and Betulaceae were simultaneously ecto- and vesicular-arbuscular mycorrhizal (VAM). Fruiting bodies of the known ectomycorrhizal fungal genera *Cortinarius*, *Lactarius*, and *Russula* were collected in late fall. Furthermore, the cosmopolitan ectomycorrhizal taxon *Cenococcum geophilum* was associated with trees and shrubs in all fens and bogs. VA-mycorrhizal fungi were not found in any of the dominant herbaceous plant species in these peatlands; however, vesicles suggesting the presence of VAM fungi were found in *Calamagrostis canadensis* in the riverine marsh and *Rubus chamaemorus* in the bog. Neither *Carex* species in fens and marshes, nor *Typha latifolia* in the lacustrine marsh were mycorrhizal; however, microsclerotia, sclerotial plaques, septate, aseptate, and clamped hyphae were observed to grow on and within cortical cells of their roots. Many of these hyphae were dematiaceous and may belong to the *Mycelium radicis atrovirens* complex (MRA), partially consisting of species in the endophytic fungal genera *Phialocephala* and *Leptodontidium*. Hyphae resembling *Rhizoctonia* were also observed, although definitive identifications were not attempted. The ecological significance of MRA genera remains largely unknown. Thus, the dominant vegetation in southern boreal bogs and fens is mycorrhizal, possibly enabling these plant species to proliferate in these nutrient-poor ecosystems by accessing otherwise unavailable nutrient pools. In contrast, marsh vegetation is generally non-mycorrhizal, possibly due to higher surface-water nutrient concentrations and fluctuating water levels.

Future research

While I investigated filamentous microfungi involved in the decomposition of above- and belowground plant litters in two peatlands, encompassing ascomycetes, basidiomycetes, fungi imperfecti, and zygomycetes, I did not investigate chytridiomycetes, yeasts, and aquatic hyphomycetes, and I was unable to identify *mycelia sterilia* in this study. Chytridiomycetes are important plant saprophytes in many aquatic and semi-aquatic ecosystems, involved in the decomposition of plant materials (Powell 1993). Similarly, aquatic hyphomycetes perform essential decomposition processes in aquatic systems (Chauvet and Suberkropp 1998) and may have played an important role decomposing the *Carex* and *Salix* litters in the riverine sedge fen, which had water levels well above the peat surface for much of the growing season. Yeasts have been isolated but rarely identified in studies investigating the mycota of peat or plants in the past, yet they, too, have been implicated to play significant roles in the degradation of organic matter (Nilsson et al. 1992, Tokumasu 1994). Similarly, every investigation into the mycota of peat and/or plant materials has resulted in the isolation of sterile fungi, often at significant frequencies (Nilsson et al. 1992, Tokumasu 1994). Some of these have been described; however, the majority is discounted and their role in the decomposition of litters remains unknown. Collaboration among experts in the identification of yeasts, aquatic hyphomycetes, and chytridiomycetes and the use of molecular techniques to identify *mycelia sterilia* would result in a more comprehensive understanding of the fungal communities of not just peatlands, but any ecosystem.

Gorham (1994) indicated that a link needs to be established between abiotic and biotic variables for global or regional climate models to predict effectively future environmental changes due to global warming. Global warming is predicted to have significant changes on many ecosystems, including peatlands, such as increasing atmospheric and soil temperatures, decreasing water tables, increased aeration of the peat, changes in plant communities, and changes in nutrient-cycling among others (Gorham 1994). The influence of these abiotic variables on biotic variables, such as communities of fungi, bacteria, and invertebrates involved in the cycling of nutrients in all ecosystems, remains poorly studied. For example, it is important to understand the effects of abiotic variables on microbial community dynamics, such as production, biomass, physiological processes, reproduction, and growth rates, to be able to include responses of microbial communities to a changing environment. In addition, the microbial communities of peatlands are poorly known and additional surveys need to be conducted in different peatlands at different geographical and site specific locations, depths, and times throughout the year. These surveys need to examine the entire spectrum of microbial communities, requiring selective isolation techniques using a series of isolation media.

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APPENDIX 1. *ARMILLARIA SINAPINA* IN HERBACEOUS PLANT MATERIAL FROM A PEATLAND IN ALBERTA, CANADA [3]

INTRODUCTION

Species of *Armillaria* (Fr.: Fr.) Staude (Agaricales, Tricholomataceae) are some of the most important tree and shrub pathogens, causing root and butt rot in many forest, orchard, and ornamental plant species worldwide (Raabe 1962, Shaw III and Kile 1991). This taxon consists of a complex of reproductively isolated groups, or biological species, in North America (NABS) (Anderson and Ullrich 1979, Anderson et al. 1980), Europe (Korhonen 1978), and Australia (Kile and Watling 1983). Currently, nine biological species are recognized in North America. Of these, only three have been found in the Canadian prairie provinces (Mallett 1990), of which *Armillaria ostoyae* (Romagn.) Herink (NABS I) and *Armillaria sinapina* Bérubé & Dessur. (NABS V) are most frequently encountered (Mallett 1992).

In an investigation of the microfungal communities of living and decomposing peatland vegetation, six fungal isolates were obtained that produced rhizomorphs in culture and resembled *Armillaria*. Surveys for conspicuous, epigeous basidiomes of *Armillaria* were unsuccessful in the fen and the surrounding uplands (within a 100 m radius from the location where the isolates were obtained) in the fall of 1998 and 1999. Therefore, the focus of this note is to outline the identification process of these six isolates, report on two new IGS-1 fragment patterns obtained from the six *Armillaria* isolates, and address the ecology and distribution of species of *Armillaria* in peatlands.

METHODS

Study area and site description

The riverine sedge fen (54° 28'N, 113° 18'W) lies within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). The climate of the area is characterized by mild summers and cold, snowy winters with a long-term mean annual temperature of 1.7 °C, and a total mean annual precipitation of approximately 500 mm (Environment Canada 1982).

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[3] A version of this chapter has been published: Thormann, M. N., C. L. Myrholm, and K. I. Mallett. 2001. *Armillaria sinapina* in herbaceous plant material from a peatland in Alberta, Canada. Canadian Journal of Botany **79**: 643-647.

The fen is dominated by *Carex aquatilis* Wahlenb., *Carex lasiocarpa* Ehrh., *Salix planifolia* Pursh, and *Equisetum fluviatile* L. The bryophyte stratum is sparse and discontinuous, consisting primarily of *Brachythecium mildeanum* (Schimp.) Schimp. *ex* Milde and *Tomenthypnum nitens* (Hedw.) Loeske. The surface water of the fen has a pH of 6.7, the mean growing season (May-October) water level is 1 cm above the peat surface, and the depth of the acrotelm (oxygenated peat horizon) is 6 cm. The fen has 1 m of peat, consisting primarily of sedge remains. A more detailed treatise of this fen is in Thormann et al. (1999) and Chapter 2.

Isolates

The microfungus communities of the dominant vegetation of a southern boreal peatland in Alberta, Canada, were investigated in a related study (Chapter 3). Briefly, the top 10 cm of ten *Carex aquatilis* leaves, ten 10 cm segments of living *C. aquatilis* rhizomes, ten entire *Salix planifolia* leaves, and ten 10 cm terminal segments of *S. planifolia* roots were collected in early May, July, and September 1997 in the riverine sedge fen. A two-year decomposition study using nylon mesh bags (3 x 6 cm, 1 mm gauge) was initiated in early September 1997 (Thormann et al. 2001, Chapter 2). Between five and eight individual fresh segments of each plant substrate were placed separately into each of 18 decomposition bags. These were deployed in the peatlands and placed horizontally approximately 2-5 cm below the peat surface (*Carex aquatilis* rhizomes and *Salix planifolia* roots) or on top of the peat surface (*S. planifolia* and *C. aquatilis* leaves) to mimic natural conditions of decomposition for these plant tissues. The bags containing the *Carex* litters were deployed in the central sedge-dominated area of fen, while the bags with the *Salix* litters were deployed in the shrub-dominated fringe area of the fen. Sets of triplicate decomposition bags of each litter were retrieved after 20 and 50 days in 1997, after eight and 12 months in May and September 1998, respectively, and after 20 and 24 months in May and September 1999, respectively.

All plant materials were cleaned by removing roots and other plant tissues using fine forceps and a dissecting microscope. Each of ten randomly selected plant segments of each plant tissue was cut with a flame-sterilized scalpel into approximately ten smaller segments (approximately 5 x 5 mm in size). These were then surface-sterilized for five minutes in 10% hydrogen peroxide and washed with sterilized distilled water (d-H_2O) prior to placing them onto primary isolation plates containing potato dextrose agar (PDA, 39.0 g Difco potato dextrose agar, 1.0 L d-H_2O) amended with benomyl (selective against most ascomycetes and deuteromycetes, 0.0002% w v^{-1}) and oxytetracycline (to suppress bacterial growth, 0.01% w v^{-1}). Six rhizomorph-forming isolates resembling *Armillaria* were obtained from different plant segments from different primary isolation plates, suggesting that these isolates were different genets of *Armillaria*. These isolates subsequently were transferred onto 1.5% malt extract agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) and maintained on that medium on a slant culture at 4 °C. Attempts to induce basidiome formation *in vitro* using autoclaved oranges and an alternating regime of light/room temperature and darkness/10°C (Guillaumin et al. 1989) were unsuccessful. Representative *Armillaria* cultures from each of the three different plant materials (living *Carex aquatilis* rhizomes, and decomposing *C. aquatilis* leaves and *Salix planifolia* leaves) have been deposited in the University of Alberta Microfungus Collection and Herbarium (UAMH) and at the Northern Forestry Centre (NoF).

Species identification

Molecular studies

The PCR-based method used to identify the *Armillaria* isolates by RFLP in the rDNA IGS-1 region was modified from the protocol established by Harrington and Wirgfield (1995). Isolates were grown for 2-3 weeks on 2% malt yeast extract agar (MYEA, 20.0 g Difco malt extract agar, 2.0 g yeast extract, and 15.0 g Difco agar, 1.0 L d-H_2O) at room temperature. Approximately 25 mm^3 of fungal mycelium was taken from the plate, added to a 1.5 ml micro centrifuge tube containing 500 µL of TE buffer pH 8 (10mM of Tris-HCl pH 8, 1mM EDTA-NaOH pH 8), ground using a disposable pellet pestle, and centrifuged at 14,000 g for 10 minutes. A 1:50 dilution of the supernatant was made with sterile, distilled water to create the template DNA. The PCR reaction mixture contained 2.5 units of Taq polymerase (Biological Sciences Department, University of Alberta, Edmonton, AB), 20 mM Tris-HCl pH 8.4, 50 mM KCl, 1.5 mM $MgCl_2$, 100 µM of each dNTP, 0.25 µM of each primer, and 5 µL template DNA in a final volume of 100 µL. The primers used were LR12R (5' CTGAACGCCTCTAAGTCAGAA 3') and O-1 (5' AGTCCTATGGCCGTGGAT 3') (Canadian Life Technologies Inc., Burlington, ON). Two to three drops of mineral oil was used to overlay the reaction mixture in the micro centrifuge tube.

After preheating the thermocycler (Model 60, COY Laboratory Products Inc., Ann Arbor, MI) to 72 °C, tubes containing the reaction mixture were introduced. Thermocycler conditions were as follows: 50 sec ramp to 95 °C, 95 sec at 95 °C (initial denaturation) followed by 30 cycles of 80 sec ramp to 55 °C, 20 sec at 55 °C (annealing), 30 sec ramp to 72 °C, 60 sec at 72 °C (elongation), 40 sec ramp to 95 °C, and 30 sec at 95 °C (denaturation). This was followed by a final elongation cycle at 72 °C for 10 min after which the temperature was held at 4 °C until use. Following amplification, 15 µL of unpurified PCR product was digested with four units *Alu* I (Canadian Life Technologies Inc., Burlington, ON) for 16 hours at 37 °C. Ten µL of digested sample was mixed with 2 µL loading buffer (0.25% bromophenol blue, 0.25% xylene cyanole FF, 30% (v v^{-1}) glycerol in d-H_2O) and loaded into the gel. Gel electrophoresis to separate digestion products was performed on a 2% agarose gel (AG, 20.0 g agarose gel, 1.0 L d-H_2O) in Tris-boric acid-EDTA buffer pH 8 (TBE) at 5 V cm^{-1} for 1-2 hours.

Digested samples of known *Armillaria* species with predetermined fragment lengths (supported by sequences published by Anderson and Stasovski (1992)) and a 50 base pair (bp) DNA ladder standard (Canadian Life Technologies Inc., Burlington, ON) were run alongside the "unknown" samples on AG. Gels were stained with ethidium bromide (0.5 µg ml^{-1}) for 30-45 min, visualized using UV light, and photographed. The lengths of the fragments were determined by comparing their migration distances to those of the known *Armillaria* species and the DNA standard. Only fragments larger than 100 bps were scored.

Inter-specific somatic incompatibility

The L-DOPA technique of Hopkin et al. (1989), based on inter-specific somatic incompatibility ("black-line"), was used for species identification. Three of the unknown isolates (1, 4, and 6) representing the three banding patterns obtained by RFLP were identified by this means. A 5 mg L^{-1} solution of L-DOPA (L-3, 4-dihydroxyphenalanine, Sigma Chemicals, St. Louis, MO) was used to intensify the "black line" produced between incompatible colonies. *Armillaria ostoyae* (NoF-1076), *Armillaria gallica* Marxmüller & Romagn. (NoF-735), *Armillaria sinapina* (NoF-758), and *Armillaria calvescens* Bérubé & Dessur. (NoF-1468), isolated from basidiomata and whose identity had been determined by haploid-haploid crosses, were paired with the unknown isolates. Pairings were replicated twice.

Diploid-haploid pairing method

The diploid-haploid pairing method of Korhonen (1978) was used to confirm identification of isolates 1, 4, and 6. Two haploid "testers" of *Armillaria ostoyae* (C-970, C-940), *Armillaria gallica*, (C-971, C-1191), *Armillaria sinapina* (C-964, C-983), and *Armillaria calvescens* (C-945, C946) were paired with the three "unknown" isolates on MEA (recipe as above) and allowed to grow for one month. The resulting colonies were observed for evidence of conversion, *i.e.* the formation of a continuous "crustose" colony type indicating that the unknown was the same species as the tester.

RESULTS AND DISCUSSION

Identification of the isolates

I obtained over 3000 fungal isolates during the investigation of the fungal communities of living and decomposing peatland vegetation from Sept. 1997 to Sept. 1999. Among these, *Armillaria* was represented six times, once from living *Carex aquatilis* rhizomes, twice from decomposing *C. aquatilis* leaves and three times from decomposing *Salix planifolia* leaves (Appendix 1 - Table 1). These isolates were identified as *Armillaria sinapina* using RFLP and confirmed by inter-specific somatic incompatibility and interfertility techniques.

Using the *Alu* I restriction enzyme, three distinct fragment patterns were obtained from the six isolates. These consisted of 399-240-183 bps ("b"), 399-240-183-135 bps ("g"), and 399-240-135 bps ("i") (Appendix 1 - Table 1). White et al. (1998) and Banik et al. (1996) have previously reported pattern "b" for *Armillaria sinapina*; however, the other two patterns have never been reported in the literature. White et al. (1998) found *A. sinapina* to be the most variable *Armillaria* species in its fragment patterns, obtaining five different fragment patterns from 17 isolates from British Columbia, Canada. Pattern "g" was a composite of the other two patterns and possibly represents a heterozygote resulting from mating of haploids with patterns "b" and "i" as described by Volk et al. (1996) for *Armillaria nabsnona* Volk & Burdsall. Based on Anderson and Stasovski's (1992) sequence data for *A. sinapina* and the very closely related species *Armillaria gallica* (Miller et al. 1994), *Alu* I restriction maps of the IGS-1 region are proposed consistent with the fragment patterns found in this study (Appendix 1 - Figure 1).

Inter-specific somatic incompatibility and interfertility tests confirmed the results of the molecular studies, showing that these six isolates were *Armillaria sinapina*. At least one of the isolates originating from decomposing *Salix planifolia* leaves (4) appeared to be haploid based on the results of its pairing with a known *A. sinapina* haploid. Both isolates in this pairing changed from individual, definitely fluffy colonies to a single suppressed "crustose" colony type. The other two paired isolates (1 and 6) appeared to be diploid, suggesting that they have the potential to produce basidiomes and that nearby living *Salix* and *Betula* shrubs and *Picea* trees may have been colonized by *A. sinapina*. However, no basidiomes were found and I did not investigate the presence of *Armillaria* rhizomorphs in their roots or stems, because I did not anticipate to isolate species of *Armillaria* from the vegetation in this fen.

Ecological implications

This is the first report of an annulate *Armillaria* species in a peatland. *Armillaria ectypa* (Fr.) Lamoure, an exannulate species of *Armillaria*, represents an exception to the generally accepted rule that species of *Armillaria* are absent from purely organic soils, as it is found exclusively in European bogs (Zolciak et al. 1997). Morrison (1982) showed that an increasing organic matter content in soil resulted in increased growth and branching of *Armillaria mellea* rhizomorphs, which he attributed, in part, to increased access to nutrients by the fungus. However, the organic matter content of his soils did not exceed 8%, unlike the soil in the riverine sedge fen, which consists of nearly 100% organic matter. Hintikka (1974) reported that, in Finland, *A. mellea* rhizomorphs are absent from organic soil horizons, except in areas with shallow peat deposits and flowing ground water. He did not provide an explanation for the absence of this plant pathogen in organic soils; however, low nutrient concentrations common to most peatlands may restrict the growth and dispersal of *Armillaria* species. Generally, peatlands are characterized by low concentrations of available nutrients such as nitrogen, phosphorus, and mineral ions (Szumigalski and Bayley 1997, Thormann and Bayley 1997), all of which have been shown to affect the growth and dispersal of *Armillaria* species (Mallett and Maynard 1998).

The growth of species of *Armillaria* is negatively affected by low soil oxygen concentrations (Smith and Griffin 1971, Shaw III and Kile 1991). Most of the isolates obtained in this study originated from decomposing plant leaf litters (five of six) that were placed on the surface of the peat. Therefore, *Armillaria sinapina* was not limited by low oxygen concentrations (depth of acrotelm is 6 cm), despite being submerged for part of the year (*e.g.*, in the spring following snow and ice melt) (mean growing season water level is 1 cm above peat surface). One isolate originated from living *Carex aquatilis* rhizomes. These rhizomes are located predominantly within the top 10 cm of the peat profile and have aerenchyma tissues that facilitate the diffusion of oxygen from above- to belowground plant tissues (roots and some rhizomes) (Fagersted 1992). Wargo and Shaw III (1985) and Whiting and Rizzo (1999) determined that moist soil conditions favour the formation of rhizomorphs; however, Smith and Griffin (1971) determined that rhizomorph growth was inhibited in water-saturated soils. Therefore, it is not surprising that I did not find rhizomorphs associated with living and decomposing plant material in the fen, where the water level is above the peat surface for most of the year.

Klein-Gebbinck and Blenis (1991) found *Armillaria ostoyae* rhizomorphs attached to and infecting herbaceous plant species (*Epilobium angustifolium* L. and *Arctostaphylus uva-ursi*

(L.) Spreng.) *in situ*. Klein-Gebbinck et al. (1993) later determined that *Armillaria mellea* (Vahl: Fr.) Kumm. and *A. ostoyae* were able to colonize roots of *E. angustifolium in vitro*. They hypothesized that herbaceous plant species may be involved in the epidemiology of *Armillaria* root disease by serving as an inoculum reservoir. The role of *Armillaria sinapina* in this fen is unclear because of the absence of woody plant material; however, what is relevant is that *A. sinapina* was isolated from living and decomposing herbaceous plant litters, indicating that it can colonize these litters and that they may serve as inocolum sources or biomass reservoirs. Furthermore, species of *Armillaria* synthesize a suite of enzymes, including polyphenol oxidases and proteases, that permits them to parasitize trees and shrubs or acquire nutrients saprophytically from accumulating litter in ecosystems (Mallett and Colotelo 1984). Therefore, it is not surprising that I isolated this basidiomycete from different plant litters as well.

Terashita and Chuman (1987, 1989) isolated several species of *Armillaria* (*A. borealis* Marx. & Korh., *A. gallica* (identified as *A. lutea* Gillet), *A. cepestipes* Velen., *A. mellea*, and *A. tabescens* (Scop.: Fr.) Emel.) from roots of the orchid *Galeola septentrionalis* Rchb. f. in Japan. The basidiomycete formed pelotons in the roots of the orchid and was mutualistic. This suggests that some species of *Armillaria* can not only colonize roots of herbaceous plant species, but can form mutualistic relationships with their plant hosts as well. It is possible that a similar relationship exists between *Armillaria sinapina* and *Carex aquatilis* rhizomes in this fen.

The majority of surveys for *Armillaria* species have been concentrated in forest ecosystems due to the potentially devastating effects this fungus can have on the forest industry (Hiratsuka 1987, Mallett 1992). While the majority of the *Alu* I restriction enzyme fragment patterns of species of *Armillaria* likely have been found in forest ecosystems (Harrington and Wingfield 1995), there may well be many additional fragment patterns from *Armillaria* species in non-forest ecosystems, such as peatlands, suggesting a high molecular diversity of individual North American and European biological species. The presence of *Armillaria sinapina* not only in herbaceous plant material but also in a peatland suggests that its distribution is more widespread than previously thought and surveys for species of *Armillaria* should include ecosystems other than forests and their woody plant substrata. Approximately 16% of Alberta's (Vitt et al. 1996) and 14% of Canada's (National Wetlands Working Group 1988) landbase is covered by peatlands. Thus, these ecosystems may represent vast biomass and genetic diversity reservoirs for species of *Armillaria* and have to be considered in future surveys.

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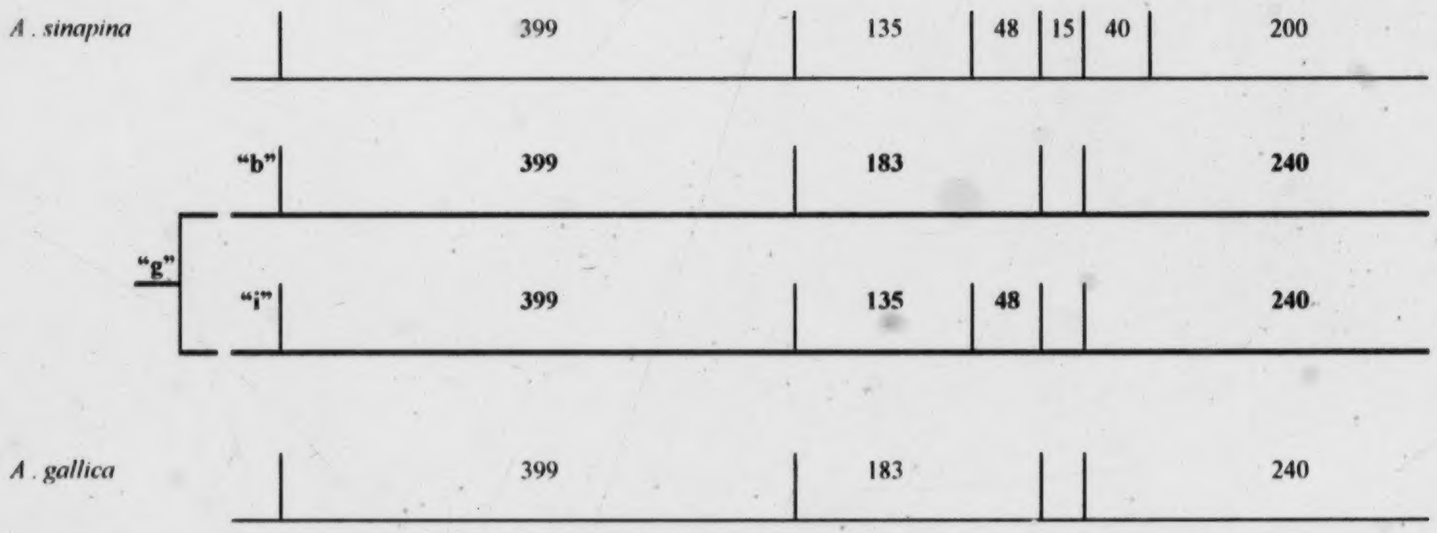

A . sinapina
399
135
48
15
40
200
"b"
399
183
240
"g"
"i"
399
135
48
240
A . gallica
399
183
240

Appendix 1 - Figure 1. IGS-1 restriction maps for *Armillaria sinapina* and the closely related *Armillaria gallica* using the *Alu* I restriction enzyme. Light lines are based on sequences published by Anderson and Stasovski (1992), **bold** lines represent the three restriction patterns seen in the six isolates from this study ("b", "i", and its composite "g"). Numbers designate the approximate fragment lengths (bps).

Appendix I - Table 1. Isolation substrates, fragment length patterns and identification letters, and accession numbers for the six isolates of *Armillaria sinapina*. All isolates originated from a riverine sedge fen in southern boreal Alberta, Canada.

Substrates	Fragment sizes (bps)	Accession numbers
Carex aquatilis rhizomes (living, Sept. 1997)	399 - 240 - 135, "i"	NoF 2380, UAMH 9792
C. aquatilis leaves (decomposing for 20 days, Oct. 1997)	399 - 240 - 183, "b"	NoF 2378
C. aquatilis leaves (decomposing for 20 months, May 1999)	399 - 240 - 183, "b"	NoF 2376
Salix planifolia leaves (decomposing for 20 months, May 1999)	399 - 240 - 183, "b"	NoF 2375
S. planifolia leaves (decomposing for 20 months, May 1999)	399 - 240 - 183, "b"	NoF 2377
S. planifolia leaves (decomposing for 20 months, May 1999)	399 - 240 - 183 - 135, "g"	NoF 2379

Note: NoF = Northern Forestry Centre, UAMH = University of Alberta Microfungus Collection and Herbarium.

APPENDIX 2. MICROFUNGI FROM *SPHAGNUM FUSCUM* FROM A SOUTHERN BOREAL BOG IN ALBERTA, CANADA [4]

INTRODUCTION

Bogs and fens are the dominant peatland types in western Canada (Vitt et al. 2000). As a landform, peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and approximately 16% of Alberta's land surface (Vitt et al. 1996). Many of these peatlands are dominated by species of *Sphagnum*, which have the ability to acidify their surroundings and hold large quantities of water (Vitt and Andrus 1977). Both of these factors contribute, in part, to decreased decomposition rates and consequently the build-up of peat in peatlands. Of the 21 known *Sphagnum* species in Alberta, *Sphagnum fuscum* (Schimp.) Klinggr. is one of the most common species and the dominant hummock-forming bryophyte species in continental bogs (Vitt and Andrus 1977). The majority of peat that accumulates in western Canadian bogs consists of *Sphagnum*-peat and because of the importance of peatlands to the global carbon cycle (Gorham 1991), it is important to understand the mycota involved in the decay of peat. Thus, investigations into the fungal assemblages of *Sphagnum* species may provide a better understanding of the dynamics of carbon in peatlands.

Many fungi are cosmopolitan, but they may be either host-specific or quantitatively more common on living or decaying vegetation (Felix 1988). Habitat selectivity apparently is attributed to changes in litter quality throughout the process of decomposition, because desirable nutrients, such as nitrogen, phosphorus, or simple sugars, become scarce, while more complex structural polymers, such as lignin and lignocellulose, become comparably more dominant in the litter (Deacon 1984). This leads to a succession of fungi in the plant litter. For example, basidiomycetes may dominate ascomycetes during the latter stages of decomposition, because they may be able to synthesize the enzymes required for the degradation of complex polymers (Deacon 1984).

In light of the dominance and importance of *Sphagnum fuscum* in bogs (Thormann and Bayley 1997), it is surprising that little is known about the fungi associated with this species. As part of a larger research project, I isolated in pure culture a series of fungi from living and decomposing *S. fuscum* from a southern boreal bog in Alberta, Canada. This paper provides an account of microfungi isolated from *S. fuscum* as well as brief annotations of these fungi.

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[4] A version of this appendix has been submitted for publication: Thormann, M. N., R. S. Currah, and S. E. Bayley. Microfungi from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. The Bryologist.

METHODS

The Perryvale bog (58° 28' N, 113° 16' W) lies within the Subhumid Low Boreal ecoclimate region of Canada (Ecoregions Working Group 1989) and is dominated by *Picea mariana* (Mill.) BSP., *Vaccinium vitis-idaea* L., *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Sphagnum fuscum*. A more detailed site description with respect to vegetation composition and surface water chemistry is elsewhere (Thormann et al. 1999b, Thormann et al. 2001, Chapters 2 and 6).

The top 3 cm of approximately 20 individual, healthy-looking, living *Sphagnum fuscum* plants were collected in early May, July, and September 1997. A two-year decomposition study using nylon mesh bags (3 x 6 cm, 1 mm gauge) was initiated in early September 1997. Between five and eight individual fresh *S. fuscum* plants (top 3 cm) were placed into each of the decomposition bags. These bags were returned to the bog and placed horizontally approximately 2 cm below the moss surface. Sets of triplicate decomposition bags with decomposing *S. fuscum* were retrieved after 20 and 50 days in 1997, after eight and 12 months in May and September 1998, respectively, and after 20 and 24 months in May and September 1999, respectively.

The *Sphagnum fuscum* was cleaned by removing roots and other plant tissues using fine forceps and a dissecting microscope. Each of ten randomly selected and cleaned segments of *S. fuscum* was cut with a flame-sterilized scalpel into approximately 10 smaller segments (approximately 5 x 5 mm in size). These were surface-sterilized for five minutes in 10% hydrogen peroxide (H_2O_2) and washed with distilled water (d-H_2O) prior to placing them on Potato Dextrose Agar (PDA, 39.0 g Difco potato dextrose agar, 1.0 L d-H_2O), PDA with rose bengal (0.03%, a general fungal growth inhibitor), PDA with benomyl (0.0002%, selective for basidiomycetes), and Mycobiotic agar® (MYC, containing cycloheximide, 35.6 g Difco mycobiotic agar, 1.0 L d-H_2O, selective for human pathogenic fungi). All media were amended with oxytetracycline (0.01%) to suppress bacterial growth. Plates were incubated at room temperature in the dark and fungi were sub-cultured onto Malt Extract Agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) as soon as they grew from the plant material. For identification purposes, slide cultures (Sigler 1993) on mixed cereal agar (Pablum®, H. J. Heinz Company of Canada Ltd., 100.0 g mixed cereal, 15.0 g Difco agar, 1.0 L d-H_2O) were prepared, mounted in polyvinyl alcohol and lactofuchsin, and examined on an Olympus BX50 compound microscope.

Morphological dimensions are given as means with ranges as "(smallest dimension)-mean dimension-(largest dimension)". Means are based on ≥10 measurements in all cases. This notation style provides an indication of the minimum, mean, and maximum sizes of relevant morphological characters and differs from the traditional style, which usually provides only a range of sizes without indicating the mean sizes of morphological characters. Only distinguishing morphological and/or cultural characteristics for each taxon are provided in the annotations. This permits the separation of each taxon from closely related taxa within the same genus isolated in this study. Information on the distribution, sources of isolates, and enzymatic capabilities of fungal taxa is provided where such data could be found. Enzymatic tests for cellulase, polyphenol oxidases, amylase, and gelatinase were performed for some taxa according to Hutchison (1990). The test for laccase followed Stalpers (1978).

Isolates were scored as separate records if they originated from different *S. fuscum* segments on the same primary isolation plate or from different primary isolation plates. Multiple isolates originating from the same plant segment on the same primary isolation plate were scored as a single record. Identified species are treated alphabetically by genus and species. *Mycelia sterilia* are listed following the identified taxa. Each annotation consists of the fungal name, full citation, and an accession number. Representative living cultures and/or permanent microscope slides have been deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH) and/or the University of Alberta Cryptogamic Herbarium (ALTA) and/or the Centraalbureau voor Schimmelcultures (CBS).

RESULTS AND DISCUSSION

Two hundred sixty-two isolates of fungi were obtained from living (88 isolates) and decomposing (174 isolates) *Sphagnum fuscum* from May 1997 to September 1999. I identified 45 species, including three ascomycetes, two basidiomycetes, 28 mitosporic fungi (fungi that reproduce asexually via the formation of spores, or conidia), and 11 zygomycetes (Appendix 2 - Table 1). Forty-one of the 45 species represent new records for *Sphagnum*. These 45 species represent 250 of the 262 isolates obtained from *S. fuscum* in this study. The remaining 12 isolates (< 5%) were sterile and could not be named; however, they were described based on morphological, physiological, and cultural characters. Molecular techniques may elucidate their identities or relationships to other fungal taxa.

Most of these species are common soil fungi, such as *Penicillium thomii*, *Trichoderma viride*, *Trichoderma harzianum*, *Mortierella ramanniana*, and *Mucor hiemalis* (Appendix 2 - Table 1), and are related to microfungi that have been isolated from peat in previous studies (McLennan and Ducker 1954, Thrower 1954, Christensen and Whittingham 1965, Dooley and Dickinson 1971, Dal Vesco 1974-75, Nilsson et al. 1992). Furthermore, *T. viride* and *Verticillium bulbillosum* have been isolated previously from another *Sphagnum* species, *Sphagnum magellanicum* Brid., by Dickinson and Maggs (1974) and *T. harzianum* has been shown to cause mass losses in the same *Sphagnum* species (Czastukhin 1967).

Three basidiomycetes were isolated from living *Sphagnum fuscum* (one from a May sample, *Bjerkandera adusta*; two from July samples, basidiomycete spp. 1 and 2). Only one neither of the two unidentified basidiomycete isolates produced clamp connections, as a characteristic unique to basidiomycetes; however, colony characteristics, such as cottony-wooly aerial mycelium, bleached growth medium on the colony reverse, and sweet odour, suggest their placement in the Basidiomycota. Additionally, all three taxa produce arthroconidia, a common vegetative propagule of saprophytic basidiomycetes (Hutchison 1989). Their role in living tissues of *S. fuscum* is unexplained and makes their presence a surprise. Although the focus of this investigation was microfungi, I also collected conspicuous, epigeous fruiting bodies of basidiomycetes. Most of these were fruiting bodies of known ectomycorrhizal fungi of *Picea*, such as species of *Cortinarius* and *Lactarius* (Kernaghan and Currah 1998), growing among the bog bryophyte species.

I identified only one dematiaceous fungus, *Cladosporium herbarum*, in this study (Appendix 2 - Table 1). However, other dematiaceous species, such as species of *Alternaria* Nees: Fr., *Cladosporium* Link: Fr., and *Phialophora* Medlar among others, have been isolated from peat in the past (McLennan and Ducker 1954, Thrower 1954, Christensen and Whittingham 1965, Dooley and Dickinson 1971, Dal Vesco 1974-75, Nilsson et al. 1992). Two additional isolates were dematiaceous, *Mycelia sterilia* 3 and 8; however, these could not be named.

In a related study, *Alternaria alternata* (Fr.) Keissler, *Arthrinium* state of *Apiospora montagnei* Sacc., *Geotrichum* sp. Link: Fr., a newly described species, *Scleroconidioma sphagnicola* Tsuneda, Currah & Thormann (Tsuneda et al. 2000), and an unidentified dematiaceous fungus were isolated from a necrotic patch of *Sphagnum fuscum* from the same bog (A. Tsuneda unpubl.). It is likely that *S. fuscum* from these necrotic patches harbour different suites of fungi than those of healthy-looking *S. fuscum*; however, my data are insufficient to address this hypothesis.

So far, only a small geographical area has been surveyed and generally only aboveground bryophyte tissues have been examined for fungal epi- and endophytes (Felix 1988), resulting in an incomplete picture of the richness about fungi on bryophytes. Furthermore, previous reports often provide only basic descriptive information of fungi associated with bryophytes (e.g. agarics or boletes). Alternatively, the "peat" mycota was investigated in Australian (McLennan and Ducker 1954, Thrower 1954), North American (Christensen and Whittingham 1965, Dooley and Dickinson 1971), and European (Dal Vesco 1974-75, Nilsson and Rülcker 1992, Nilsson et al. 1992) peatlands. However, peat consists of a heterogeneous assemblage of partially decomposed organic matter, including roots of different vascular plants, different mosses, and other microbes, and the specific origin of individual fungal taxa remains uncertain in those studies. Thus, neither type of study, descriptive or soil mycota studies, provides information specific enough for bryologists and mycologists concerned with the occurrences of specific fungi on/in specific bryophyte species.

Carbon constitutes approximately 48% of *Sphagnum*-derived peat (Thormann et al. 1999a). This carbon is hypothesized to be mineralized at greater than current rates under a global warming scenario, releasing CO_2 into the atmosphere (Yavitt et al. 1993), suggesting that peatlands with their significant carbon deposits may provide a positive feedback to global warming. The fungi isolated in this study have the ability to degrade a variety of carbon sources. For example, cellulose and lignin-like compounds constitute 38 and 30% of the structural polymers of *Sphagnum* or *Sphagnum*-derived peat, respectively (Yavitt et al. 1997, Turetsky et al. 2000). Twenty of 55 of my fungal taxa (36%) have the ability to utilize cellulose as a carbon source, while polyphenol oxidases, the enzymes required for the degradation of lignin and lignin-like substances, can be synthesized by nine of my taxa (16%). Therefore, these fungi are important organisms in the mineralization of carbon in peatlands.

Twenty-one of the 55 species (38%) in this study were isolated from decomposing *Sphagnum fuscum* exclusively, while 16 of the 55 fungal species (29%) were isolated from living *S. fuscum*, and the remaining 18 species (33%) were isolated from both living and decomposing *S. fuscum* (Appendix 2 – Table 1). An annotated list of these fungi follows.

Annotated list of fungi from living and decomposing *Sphagnum fuscum*

Acremonium chrysogenum (Thisum. & Sukop.) W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 109-111 (ALTA 10669).

Conidia ellipsoidal (2.8)-3.5-(4.1) µm x (1.0)-1.5-(1.9) µm; widespread; reported from soil, decaying vegetation, marine water (Gams 1971); cellulolytic, lignolytic, utilizes fats and other carbohydrates (Gams 1971).

Acremonium cf. curvulum W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 57-59 (CBS 102853).

Colony 13-21 mm in diam. after ten days on MEA; mycelium mostly submerged and appressed, few white tufts, reverse faint creamy-yellow to faint yellow-orange; phialides simple, smooth, no collarette, tapering towards apex, (20)-44-(80) µm; conidia lightly to acutely curved, weakly apiculate at base, rounded at tip, sparsely produced, (5.0)-6.3-(8.1) µm x (1.3)-1.9-(2.2) µm; uncommon; reported from soil, water, vegetation (Gams 1971); cellulolytic, utilizes starch.

My isolates differ from *A. curvulum* because they are slower sporulate, have scant aerial mycelium, and less intense colouration of the medium. Conidial and phialidic dimensions and growth rates are close to *A. curvulum*. My isolates were used in a study investigating the cell wall degradation of *Sphagnum fusucm* (Tsuneda et al. 2001).

Acremonium strictum W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 42-44 (ALTA 10670).

Conidia cylindrical, (4.0)-4.4-(5.7) µm x (0.9)-1.5-(2.0) µm; cosmopolitan; reported from soil, vegetation, wood, fungi, dung, jet fuel, aquatic habitats, human tissues, and air (see Domsch et al. 1980 for references); cellulolytic, gelatinolytic.

Aspergillus niger van Tieghem, 1867, Annales des Sciences Naturelles. A. Botanique, Séries 5, **8**: 240 (ALTA 10673).

Conidia globose, verrucose, (3.5)-4.8-(5.4) µm; cosmopolitan; reported from soil, animals, human tissues, foods, decaying vegetation, and air (see Domsch et al. 1980 and Klich and Pitt 1994 for references); able to utilize a wide array of substrates, including chitin (Kawasaki and Ito 1964) and starch (Barton et al. 1972).

Aspergillus versicolor (Vuill.) Tiraboschi, 1908/09, Annali di Botanica, Roma 7: 9 (ALTA 10674).

Conidia globose, echinulate, (2.2)-2.7-(3.0) µm; cosmopolitan; reported from soil, vegetation, animals, water, and foods (see Domsch et al. 1980 for references); weakly cellulolytic (Reese and Downing 1951), utilizes starch (Franz 1975) and other carbohydrates (Trique 1968).

Basidiomycete sp. 1 (ALTA 10853).

Colonies 83 and 74 mm in diam. after seven days on MEA and PDA, respectively, reverse bleached; aerial mycelium white, patchy, floccose; hyphae smooth, hyaline, 2.0-4.0 µm in diam.; clamp connections abundant; conidiophores absent or micronematous; arthroconidia hyaline, abundant, dry, aseptate, smooth, various shapes (rectangular, barrel-shaped, curved, edges rounded when mature), (4.0)-6.0-(16.0) µm x (2.0)-3.0-(4.0) µm; chlamydospores absent; odour sweet; exudate clear to golden-yellow, abundant, among aerial hyphae; isolated on PDA and PDA with benomyl; polyphenol oxidase negative, laccase positive.

Basidiomycete sp. 2. (ALTA 10854).

Colonies 85 and 80 mm in diam. after seven days on MEA and PDA, respectively, colony reverse not bleached; aerial mycelium white, patchy; hyphae hyaline, smooth, 2.5-4.0 µm in diam.; clamp connections absent; conidiophores absent or micronematous; arthroconidia hyaline, abundant, dry, aseptate, smooth, various shapes (rectangular, barrel-shaped, curved, branched, edges rounded when mature), abundant, dry, (3.0)-4.5-(6.0) µm x (2.0)-2.5-(3.0) µm; chlamydospores absent; odour absent; exudate absent; isolated on PDA with rose bengal; polyphenol oxidase negative, laccase positive.

Bjerkandera adusta (Willd.: Fr.) Karst., 1879, Meddelanden af Societas pro Fauna et Flora Fennica 5: 38.

Mycelium white, cottony-wooly, colony reverse bleached; arthroconidia hyaline, rectangular, abundant, dry, (5)-9-(13) µm x (2.5)-3.0-(3.5) µm; odour strong, sweet; cosmopolitan; from wood (Stalpers 1978); polyphenol oxidase positive, laccase positive (Stalpers 1978).

The presence of simple septa, the bleached colony reverse, strong odour, and a positive reaction for laccase separate this basidiomycete from other arthroconidial basidiomycetes (Stalpers 1978) and the hyphomyceteous mycoparasite *Geotrichopsis mycoparasitica* Tzean &

Estey (Tzean and Estey 1991). Additionally, exudate absence, bleached colony reverse, sweet odor, clamp connection presence, and polyphenol oxidase synthesis separates *B. adusta* from basidiomycetes 1 and 2.

Botrytis cinerea Pers. *ex* Pers., 1822, Synopsis Methodica Fungorum, p. 690 (ALTA 10676).

Macroconidia pale brown, obovoid, smooth-walled, often with protuberant hilum, (10)-11-(13) µm x (5)-6-(7) µm; microconidia globose, (2.4)-2.8-(3.2) µm; cosmopolitan; reported from vegetation, animal tissues, air, and soil (see Domsch et al. 1980 for references); cellulolytic (Basu and Ghose 1960) and pectinolytic (Domsch and Gams 1969) among others (see Domsch et al. 1980 for references).

Cladosporium herbarum (Pers.) Link *ex* Gray, 1821, Natural Arrangement of British Plants I, p. 556 (ALTA 10678).

Conidia ellipsoidal to cylindrical, ends rounded, verruculose, scars prominent, (2)-8-(16) µm x (2)-3-(4) µm; cosmopolitan; reported from vegetation, soil, aquatic habitats, dung, animal tissues, air, and food (see Domsch et al. 1980 for references); cellulolytic (Marsh et al. 1949), pectinolytic (Domsch and Gams 1969), utilizes starch (Domsch 1960).

Fusarium aquaeductuum var. *medium* Wollenw., 1931, Fusarium-Monographie: Fungi Parasitici et Saprophytici, p. 556 (ALTA 10680).

Phialides simple or branched near the base, septate, (58)-80-(119) µm; macroconidia curved to (sometimes) straight, (usually) tri-septate, (38)-44-(52) µm x (3.8)-4.3-(5.0) µm; microconidia ellipsoidal to slightly curved, (sometimes) septate, (6)-7-(10) µm x (1.5)-1.8-(2.0) µm; cosmopolitan; reported from water, sewage, fungal sporocarps, peat (see Domsch et al. 1980 for references); cellulolytic (Gersonde and Kerner-Gang 1968), utilizes polyphenolics (Barz et al. 1976).

Kernia retardata Udagawa and Muroi, 1981, Transactions of the Mycological Society of Japan **22**: 18 (UAMH 9613).

Ascomata black, spherical to pyriform, without neck, (140)-185-(250) µm; ascospores reddish-brown, single-celled, reniform, smooth, (5.0)-5.4-(6.0) µm x (3.0)-4.3-(5.0) µm; widespread; reported from decaying vegetation, foods, soil, dung (Lumley et al. 2000); cellulolytic, gelatinolytic, utilizes starch.

Anamorph a *Scopulariopsis*; conidia (4.0)-5.9-(7.0) µm x (2.0)-2.3-(2.5) µm (ALTA 10703).

Monocillium constrictum W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), p. 164-165 (ALTA 10685).

Colony faint orange to ochre; phialides simple, densely arranged along hyphae, (8)-11-(19) µm; conidia slightly curved, apex rounded, base apiculate, (4)-5-(6) µm x (1.0)-1.4-(1.7) µm; cosmopolitan; reported from plants, air, fungal sporocarps (see Gams 1971 for references); cellulolytic, gelatinolytic, utilizes tannic acid and starch.

Mortierella alpina Peyronel, 1913, Dissertationes Padova (ALTA 10686).

Sporangiophores simple, swollen at the base; sporangiospores ellipsoidal to cylindrical, (3.5)-4.1-(5.0) µm x (1.5)-2.2-(2.5) µm; cosmopolitan; reported from soil (see Domsch et al. 1980 for references); chitinolytic (Domsch 1960), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella elongata Linnem., 1941, Pflanzenforschung **23**: 43 (ALTA 10687).

Sporangiophores simple or branched near the base; sporangiospores ellipsoidal to short-cylindrical, (6.0)-8.2-(10.0) µm x (3.0)-4.5-(6.0) µm; cosmopolitan; reported from soil, rhizosphere of plants (see Domsch et al. 1980 for references); weakly pectinolytic (Domsch and Gams 1969), chitinolytic (Jackson 1965), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella horticola Linnem., 1941, Pflanzenforschung **23**: 21 (ALTA 10691).

Sporangiophores simple or with one side-branch; sporangiola spherical to globose, spinulose, (8)-11-(15) µm; cosmopolitan; reported from soil, roots of herbaceous plants (see Domsch et al. 1980 for references); chitinolytic (Jackson 1965).

Mortierella humilis Linnem., 1936, Flora **130**: 176-217 (ALTA 10692).

Sporangiophores branched near the base; sporangiola spherical to globose, finely verrucose, (7)-11-(15) µm; cosmopolitan; reported from a variety of soils and compost (see Domsch et al. 1980 for references); chitinolytic (Gray and Baxby 1968), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella isabellina Oud. & Koning, 1971, Archives Neerlandaise des Sciences Exactes et Naturelles, Séries **7**: 266-298 (ALTA 10689).

Sporangiophores simple or branched; sporangiospores globose to slightly angular, (2.2)-2.6-(3.1) µm; cosmopolitan; reported from soil and vegetation (see Domsch et al. 1980 for references).

Mortierella minutissima van Tieghem, 1876, Annales des Sciences Naturelles. A. Botanique, Séries **4**: 385 (ALTA 10690).

Sporangiophores simple or branched near base; sporangiospores globose, (3.5)-4.0-(5.0) µm; cosmopolitan; reported from soil and wood (see Domsch et al. 1980 for references); chitinolytic (Gray and Baxby 1968), utilizes other carbohydrates (Mil'ko and Gabryushina 1968).

Mortierella ramanniana var. *angulispora* (Möller) Linnem., 1971, Pflanzenforschung **23**: 19 (ALTA 10693).

Sporangiophores simple or branched; sporangiospores angular, smooth, (2.4)-3.0-(3.6) µm; cosmopolitan; reported from soil, decaying vegetation, dung, and animal tissues (see Domsch et al. 1980 for references); pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Mortierella ramanniana var. *ramanniana* (Naumov) Linnem., 1971, Pflanzenforschung **23**: 19 (ALTA 10694).

Sporangiophores simple or branched; sporangiospores oval to ellipsoid, smooth, (2.8)-3.3-(3.8) µm; cosmopolitan; reported from soil, decaying vegetation, dung, and animal tissues (see Domsch et al. 1980 for references); pectinolytic, cellulolytic, utilizes starch (Flanagan and Scarborough 1974).

Mortierella renispora Dixon-Stewart, 1932, Transactions of the British Mycological Society **17**: 208-220 (ALTA 10695).

Sporangiophores simple, with a broad foot cell; sporangiospores globose to reniform, (1.5)-2.1-(2.5) µm x (4.0)-4.1-(4.5) µm; cosmopolitan; reported from soil (Dixon-Stewart 1932, Mehrotra and Mehrotra 1964).

Mortierella verticillata Linnem., 1941, Pflanzenforschung **23**: 22 (ALTA 10696).

Sporangiophores verticillately branched; sporangiola spherical to globose, (7)-10-(13) µm; cosmopolitan; reported from soil and roots of plants (see Domsch et al. 1980 for references); chitinolytic (Gray and Baxby 1968).

Mucor hiemalis Wehmer, 1903, Annales Mycologici **1**: 39 (ALTA 10697).

Sporangiophores simple or slightly sympodially branched, up to 1.8 cm long; sporangiospores ellipsoidal, (4.8)-5.6-(7.0) µm x (2.5)-3.1-(4.8) µm; cosmopolitan; reported from soil, vegetation, dung, and foods (see Domsch et al. 1980 for references); hemicellulolytic (Loub 1960), chitinolytic (Domsch 1960), pectinolytic (Domsch and Gams 1969), utilizes starch (Franz 1975).

Nodulisporium sp. (ALTA 10698).

Colony greyish-brown, velvety towards margin, 20 mm in diam. after seven days on MEA; conidiophores branched, (46)-118-(259) µm; conidiogenous cells (12)-18-(24) µm; conidia light brown, solitary, dry, truncate, ellipsoidal to obovoid, (3.2)-3.8-(4.1) µm x (1.3)-1.7-(2.1) µm; the genus is cosmopolitan; species are reported from herbaceous plants, wood, decomposing plant materials (Ellis 1971, Deighton 1985); cellulolytic, utilizes starch.

Oidiodendron maius Barron, 1962, Canadian Journal of Botany **40**: 600-602 (ALTA 10700, UAMH 9749).

Conidiophores (150)-260-(350) µm x (1.8)-2.8-(3.8) µm; arthroconidia hyaline, (3.0)-3.6-(4.0) µm x (1.9)-2.1-(2.2) µm; cosmopolitan; reported from soil and roots of Ericaceae (see Hambleton and Currah 1997 for references); pectinolytic, cellulolytic, utilizes starch, gelatin, and tannic acid. This isolate was used in a study on the degradation of *S. fuscum* cell walls (Tsuneda et al. 2001).

Oidiodendron scytaloides Gams & Söderström, 1983, Cryptogamie, Mycologie **4**: 239-241 (UAMH 9751).

Conidiophores (35)-75-(225) µm; arthroconidia hyaline, (2.0)-3.1-(4.0) µm x (1.3)-1.6-(1.7) µm; chlamydospores dark, ellipsoidal, finely verrucose, in terminal and intercalary series, (3.2)-4.1-(6.0) µm x (2.0)-2.9-(4.8) µm; cosmopolitan; reported from conifer forest soil (Gams and Söderström 1983); pectinolytic, utilizes starch, tannic acid.

Paecilomyces marquandii (Massee) Hughes, 1951, Mycological Papers **45**: 30 (ALTA 10855).

Diffusible yellow pigment on MEA; phialides swollen at base with long, tapering neck, (9)-11-(12) µm; conidia fusiform, in chains, (3.0)-3.6-(4.3) µm x (1.8)-2.1-(2.5) µm; cosmopolitan; reported from soil (see Domsch et al. 1980 for references); gelatinolytic (Borut 1960), chitinolytic (Jackson 1965), utilizes starch (Franz 1975).

Penicillium funiculosum Thom, 1910, Bulletin. Bureau of Animal Industry. U.S. Department of Agriculture **118**: 69 (ALTA 10856).

Conidiophores biverticillate, (59)-74-(140) µm; phialides acerose, (9)-11-(12) µm; conidia ellipsoidal to spherical, (2.5)-2.9-(3.4) µm long; cosmopolitan; reported from soil (Pitt 1988); cellulolytic (Gochenaur 1975), utilizes various sugars (Dickinson and Boardman 1970).

Penicillium montanense Christensen & Backus, 1962, Mycologia **54**: 574 (ALTA 10858).

Conidiophores monoverticillate, distinctly vesiculate, (150)-180-(240) µm; phialides ampulliform, (9)-11-(12) µm; conidia greyish turquoise, spherical, distinctly spinose, (3.2)-3.6-(4.1) µm; common; reported from bogs and conifer forests (Christensen and Backus 1962, Christensen and Whittingham 1965).

Penicillium odoratum Christensen & Backus, 1961, Mycologia **53**: 459-462 (ALTA 10857).

Conidiophores monoverticillate, distinctly vesiculate, (150)-180-(240) µm; phialides ampulliform, (7)-9-(10) µm; conidia blue, broadly ellipsoidal, distinctly rough-walled, (3.3)-3.8-(4.1) µm long; cosmopolitan; reported from peatlands, undisturbed forest soils (Christensen and Backus 1961, Pitt 1988); cellulolytic (Franz and Loub 1959), pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Penicillium purpurogenum Stoll, 1904, Beiträge zur Charakterisierung von *Penicillium* 32 (ALTA 10859).

Diffusible red pigment on Czapek's Yeast Extract agar; conidiophores biverticillate, (95)-210-(295) µm; phialides ampulliform, (8)-10-(12) µm; conidia spherical to ellipsoidal, rough-walled, (2.9)-3.2-(3.5) µm long; cosmopolitan; reported from soil (Pitt 1988); cellulolytic, pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Penicillium thomii Maire, 1910, Bulletin. Societé d'Histoire Naturelle de l'Afrique du Nord **8**: 189 (ALTA 10860).

Conidiophores monoverticillate, distinctly vesiculate, (280)-310-(370) µm; phialides ampulliform, (8)-10-(12) µm; conidia sub-spherical to ellipsoidal, rough-walled, (3.5)-4.0-(4.5) µm long; cosmopolitan; reported from decaying vegetation, foods, fungi, soil (Pitt 1988); pectinolytic (Flanagan and Scarborough 1974), cellulolytic (Jefferys et al. 1953).

Sordaria fimicola (Rob.) Ces. & de Not., 1948, Canadian Journal of Research, C, **26**: 486-497 (UAMH 9475, ALTA 10705).

Ascospores dark brown to black, single-celled, broadly fusiform to ovoid and/or subglobose, germ pore, gelatinous sheath, (20)-23-(26) µm x (10)-13-(15) µm; cosmopolitan; reported from a variety of substrates, principally the dung of herbivores and soil (see Domsch et al. 1980 for references); cellulolytic, utilizes starch.

Sporormiella intermedia (Auersw.) Ahmed & Cain, 1969, Bulletin. National Science Museum, Tokyo **12**: 311-430 (ALTA 10706).

Ascospores dark brown to black, multiseptate (typically triseptate) with constrictions at septa, gelatinous sheath, oblique germ slits, (50)-58-(65) µm x (10)-12-(13) µm; widespread; reported from herbivore and carnivore dung (Ahmed and Cain 1972); utilizes starch.

Sporothrix state of *Ophiostoma stenoceras* (Robak) Melin & Nannf., 1932, Svenska Skogsvardsforeningen Tidskrift **32**: 408 (UAMH 9753).

Conidiogenous cells simple, erect, (22)-30-(43) µm, with an inconspicuous conidiogenous denticle at apex; conidia hyaline, ovoid to fusiform, (3.2)-4.4-(5.2) µm x (1.1)-1.5-(1.9) µm; sexual state immature; cosmopolitan; reported from wood, herbaceous plants, human tissues, soil (de Hoog 1974); pectinolytic, utilizes starch, tannic acid.

Sporothrix sp. (UAMH 9752).

Mycelium hyaline when young, becoming purplish to black after 10 days on MEA, mycelium purple on cereal agar; conidiogenous cells simple, erect, (3)-7-(15) µm, conidiogenous denticle at apex, 2-3 µm wide; phialidic conidia hyaline, ovoid to fusiform, single-celled, contain large oil body, (2.0)-2.8-(3.2) µm x (1.3)-1.8-(2.0) µm; lateral conidia pale brown, abundant, globose, (1.5)-2.5-(3.2) µm. The genus is reported from soil, plants, human tissues, decomposing vegetation (de Hoog 1974); gelatinolytic, unable to utilize tannic acid, starch, or pectin.

Trichoderma aureoviride Rifai, 1969, Mycological Papers **116**: 34-38 (ALTA 10707).

Colony reverse golden to golden-yellow from needle-shaped crystals in medium; conidia obovoid, smooth, (2.2)-3.9-(4.4) µm x (1.9)-2.6-(3.1) µm; cosmopolitan; reported from soil, vegetation, cork (see Rifai 1969 for references); cellulolytic, gelatinolytic, utilizes starch.

Trichoderma harzianum Rifai, 1969, Mycological Papers **116**: 38-42 (ALTA 10708).

Conidia subglobose to oval, smooth, (2.2)-2.5-(3.0) µm; cosmopolitan; reported from soil, vegetation, paper, textiles, and jet fuel (see Domsch et al. 1980 for references); cellulolytic (Park 1976), utilizes starch (Franz 1975).

Trichoderma polysporum (Link *ex* Pers.) Rifai, 1969, Mycological Papers **116**: 18-22 (ALTA 10712).

Mycelium white, sterile hyphae extend beyond phialide apices; conidia ellipsoidal, smooth, (3.3)-3.6-(4.0) x (1.4)-1.8-(2.1) µm; cosmopolitan; reported from soil, plant litter, rhizosphere of plants (see Domsch et al. 1980 for references); cellulolytic (Park 1976), weakly chitinolytic (Jackson 1965), utilizes a variety of sugars (Danielson and Davey 1973).

Trichoderma viride Pers. *ex* S. F. Gray, 1821, Natural Arrangement of British Plants I, p. 560 (ALTA 10713).

Conidia green, globose, roughened, (3.2)-3.7-(4.1) µm; cosmopolitan; reported from soil, aquatic ecosystems, vegetation, dung, foods, and animal tissues (see Domsch et al. 1980 for references); cellulolytic (Reese and Levinson 1952), pectinolytic (Domsch and Gams 1969), chitinolytic (Domsch 1960).

Verticillium bulbillosum W. Gams & Malla, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 189-190 (ALTA 10715).

Conidia curved, in slimy heads, length variable, primary conidia often longer and more curved than secondary conidia, (2)-3-(6) µm x (1)-1-(2) µm; chlamydospores intercalary or terminal on lateral hyphae; uncommon; reported from soil, ectomycorrhizal fungi (Gams 1971); cellulolytic, gelatinolytic, utilizes starch.

Verticillium cephalosporium W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 180-181 (ALTA 10716).

Conidia globose to subglobose, (2.0)-3.3-(4.3) µm x (1.0)-1.4-(1.8) µm; uncommon; reported from soil (Gams 1971); cellulolytic, gelatinolytic, utilizes starch.

Verticillium lecanii (Zimm.) Viégas, 1939, Revue Institute Café Sao Paolo **14**: 754 (ALTA 10717).

Conidia cylindrical to ellipsoidal, in slimy heads, (3.1)-4.7-(6.5) µm x (1.6)-1.9-(2.2) µm; cosmopolitan; reported from soil, insects, plant litter (see Domsch et al. 1980 for references); cellulolytic, chitinolytic (Domsch 1960), pectinolytic, utilizes starch (Flanagan and Scarborough 1974).

Verticillium psalliotae W. Gams, 1971, *Cephalosporium*-artige Schimmelpilze (Hyphomycetes), pp. 184-186 (ALTA 10718).

Conidia sickle-shaped with pointed ends, in slimy heads, (5.2)-6.7-(8.5) µm x (1.0)-1.2-(1.7) µm; widespread; reported from fungi, dung, soil, and insects (see Domsch et al. 1980 for references); cellulolytic, gelatinolytic, utilizes starch.

Mycelium sterilium 1

Colonies 80 and 70 mm in diam. after seven days on MEA and PDA, respectively; mycelium white, patchy; hyphae hyaline, smooth, 2.5-4.0 µm in diam.; benomyl tolerant; isolated on PDA with benomyl; cellulolytic, gelatinolytic, unable to utilize cellulose, pectin, starch, or tannic acid.

Mycelium sterilium 2

Colonies 12 and 8 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium white, patchy; hyphae hyaline, septate, smooth, forming coils, 2.5-3.5 µm in diam.; isolated on PDA; gelatinolytic, utilizes starch, unable to utilize cellulose, pectin, or tannic acid.

Mycelium sterilium 3

Colonies 7 and 5 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium mouse grey, abundant; hyphae dematiaceous, septate, smooth, toruloid cells frequent, forming coils, 2.5-3.0 µm in diam.; isolated on MYC; unable to utilize cellulose, gelatin, pectin, starch, or tannic acid.

Mycelium sterilium 4

Colonies 82 and 70 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium white, scant; hyphae hyaline, septate, smooth, 4.0-5.5 µm in diam.; chlamydospores abundant, smooth, 8-10 µm; isolated on PDA; utilizes gelatin, starch, and tannic acid, unable to utilize cellulose or pectin.

Mycelium sterilium 5

Colonies 43 and 44 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium white, patchy; hyphae hyaline, septate, smooth, swollen near septa, 4.0-5.5 µm in diam.; isolated on PDA; gelatinolytic, unable to utilize cellulose, pectin, starch, or tannic acid.

Mycelium sterilium 6

Colonies 83 and 78 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium white, patchy; hyphae hyaline, septate, smooth, 2.5-3.0 µm in diam.; isolated on PDA; cellulolytic, gelatinolytic, utilizes starch, unable to utilize pectin or tannic acid.

Mycelium sterilium 7

Colonies 65 and 80 mm in diam. after seven days on MEA and PDA, respectively; aerial mycelium white, patchy; hyphae hyaline, septate, smooth, thick-walled, swollen near septa, 2.5-4.0 µm in diam.; isolated on PDA with benomyl; unable to utilize tannic acid.

Mycelium sterilium 8

Colonies 85 mm in diam. after three days on MEA and PDA; aerial mycelium white, patchy; hyphae hyaline to tan, septate, smooth, 5.5-9.0 µm in diam.; isolated on PDA with rose bengal; cellulolytic, gelatinolytic, utilizes starch, unable to utilize pectin or tannic acid.

Mycelium sterilium 9

Colonies 85 mm in diam. after three days on MEA and PDA; aerial mycelium white, patchy; hyphae hyaline, septate, smooth, forming coils, 5.0-6.0 µm in diam.; hyphae hyaline, aggregates infrequent, 25-40 μm in diam.; isolated on PDA with rose bengal; cellulolytic, gelatinolytic, utilizes starch, unable to utilize pectin or tannic acid.

Mycelium sterilium 10

Colonies 85 mm in diam. after three days on MEA and PDA; aerial mycelium white, patchy; hyphae tan, septate, smooth, 4.5-5.5 μm in diam.; hyphal aggregates tan, abundant, 50-100 μm in diam.; isolated on PDA with rose bengal; cellulolytic, gelatinolytic, utilizes starch, unable to utilize pectin or tannic acid.

CONCLUSIONS

Forty-five fungal species were identified in a systematic survey of microfungi associated with living and decomposing *Sphagnum fuscum*. Of these, 41 represent new records for fungi on *S. fuscum*. These fungi showed varying abilities to utilize a variety of carbon sources and are important organisms in the mineralization of carbon in peatlands. Undoubtedly, there are many additional fungi that are associated with this bryophyte. Alternative culturing techniques, growth media, and growth conditions in future investigations will reveal additional fungal species and ultimately add to our understanding of the mycota associated with this dominant bog bryophyte species.

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Appendix 2 - Table 1. Fungi from living and decomposing *Sphagnum fuscum*. Fungal classification is in accordance with Hawksworth et al. (1995). Numbers in brackets indicate the number of isolates obtained from living, decomposing, or living and decomposing *S. fuscum*.

Fungal classification				Substrate state
Division	Order	Family	Fungi	
Zygomycota	Mucorales			
		Mortierellaceae	*Mortierella alpina*	Decomposing (3) *S. fuscum*
			M. elongata	Living (6) and decomposing (12) *S. fuscum*
			M. horticola	Living (1) and decomposing (3) *S. fuscum*
			M. humilis	Living (1) *S. fuscum*
			M. isabellina	Living (1) and decomposing (7) *S. fuscum*
			M. minutissima	Living (7) and decomposing (10) *S. fuscum*
			M. ramanniana var. *angulispora*	Living (5) and decomposing (9) *S. fuscum*
			M. ramanniana var. *ramanniana*	Living (2) and decomposing (6) *S. fuscum*
			M. renispora	Living (2) and decomposing (4) *S. fuscum*
			M. verticillata	Living (1) and decomposing (1) *S. fuscum*
		Mucoraceae	*Mucor hiemalis*	Living (10) and decomposing (26) *S. fuscum*
Ascomycota	Dothideales			
		Sporormiaceae	*Sporormiella intermedia*	Living (1) *S. fuscum*
	Microascales			
		Microascaceae	*Kernia retardata*	Living (2) and decomposing (1) *S. fuscum*

	Sordariales			
		Sordariaceae	*Sordaria fimicola*	Living (4) *S. fuscum*
Basidiomycota	Poriales			
		Coriolaceae	*Bjerkandera adusta*	Living (1) *S. fuscum*
	Unknown		Basidiomycete sp. 1	Living (3) *S. fuscum*
			Basidiomycete sp. 2	Living (1) *S. fuscum*
Deuteromycetes	Dothideales			
		Mycosphaerellaceae (anamorphic)	*Cladosporium herbarum*	Living (1) *S. fuscum*
	Eurotiales			
		Trichocomaceae (anamorphic)	*Aspergillus niger*	Living (2) and decomposing (1) *S. fuscum*
			A. versicolor	Decomposing (1) *S. fuscum*
			Paecilomyces marquandii	Living (1) *S. fuscum*
			Penicillium funiculosum	Living (9) and decomposing (4) *S. fuscum*
			P. montanense	Decomposing (2) *S. fuscum*
			P. odoratum	Decomposing (4) *S. fuscum*
			P. purpurogenum	Living (5) *S. fuscum*
			P. thomii	Living (4) and decomposing (19) *S. fuscum*
	Hypocreales			
		Hypocreaceae (anamorphic)	*Fusarium aquaeductuum* var. *medium*	Living (1) *S. fuscum*
			Trichoderma aureoviride	Decomposing (2) *S. fuscum*
			T. harzianum	Living (1) and decomposing (2) *S. fuscum*
			T. polysporum	Decomposing (2) *S. fuscum*

			T. viride	Living (4) and decomposing (12) *S. fuscum*
	Leotiales			
		Sclerotiniaceae (anamorphic)	*Botrytis cinerea*	Decomposing (1) *S. fuscum*
	Onygenales			
		Myxotrichaceae (anamorphic)	*Oidiodendron maius*	Decomposing (1) *S. fuscum*
			O. scytaloides	Living (2) and decomposing (1) *S. fuscum*
	Ophiostomatales			
		Ophiostomataceae	*Sporothrix* sp.	Decomposing (4) *S. fuscum*
			Sporothrix state of *Ophiostoma stenoceras*	Decomposing (3) *S. fuscum*
	Trichosphaeriales			
		Trichosphaeraceae (anamorphic)	*Monocillium constrictum*	Living (1) *S. fuscum*
	Xylariales			
		anamorphic fungus	*Nodulisporium* sp.	Living (1) and decomposing (1) *S. fuscum*
Mitosporic fungi *			*Acremonium chrysogenum*	Decomposing (1) *S. fuscum*
			A. cf. curvulum	Decomposing (3) *S. fuscum*
			A. strictum	Decomposing (1) *S. fuscum*
			Verticillium bulbillosum	Living (2) and decomposing (7) *S. fuscum*
			V. cephalosporium	Decomposing (1) *S. fuscum*
			V. lecanii	Decomposing (1) *S. fuscum*
			V. psalliotae	Living (2) and decomposing (10) *S. fuscum*
Mycelia sterilia *			*Mycelium sterilium* 1	Living (1) *S. fuscum*
			Mycelium sterilium 2	Living (1) *S. fuscum*

Mycelium sterilium 3	Living (1) *S. fuscum*
Mycelium sterilium 4	Decomposing (1) *S. fuscum*
Mycelium sterilium 5	Decomposing (1) *S. fuscum*
Mycelium sterilium 6	Decomposing (2) *S. fuscum*
Mycelium sterilium 7	Living (1) *S. fuscum*
Mycelium sterilium 8	Decomposing (1) *S. fuscum*
Mycelium sterilium 9	Decomposing (1) *S. fuscum*
Mycelium sterilium 10	Decomposing (2) *S. fuscum*

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* Unknown taxonomic position.

APPENDIX 3. THE RELATIVE ABILITY OF FUNGI FROM *SPHAGNUM FUSCUM* TO MINERALIZE CARBON [5]

INTRODUCTION

Peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and approximately 16% of Alberta's land surface, of which 4.9% are bogs and the remainder are fens (Vitt et al. 1996). Bogs are ombrotrophic peatlands that receive nutrients only from precipitation and are dominated by *Sphagnum* species, *Picea mariana* (Mill.) BSP., and members of the Ericaceae. Fens are minerotrophic peatlands that receive water from precipitation and ground water sources and are dominated by sedges, shrubs, and (mostly) non-*Sphagnum* moss species (Szumigalski and Bayley 1996b, Thormann and Bayley 1997b). *Sphagnum* species are of great importance to many northern ecosystems because of their ability to acidify their surroundings, hold large quantities of water in their hyaline cells, and their slow decomposition rates (Vitt and Andrus 1977). *Sphagnum fuscum* (Schimp.) Klinggr. is the dominant hummock-forming bryophyte species in bogs (Vitt and Andrus 1977) and can also occur, although less abundantly, in fens.

Peatlands accumulate peat, a heterogeneous assemblage of partially decomposed plant materials (approximately 50% carbon), annually (Thormann et al. 1999b). Gorham (1990) estimated that northern peatlands store between 180 and 277 Gt (1 Gt = 10^9 t) of carbon, which represents approximately 10-16% of the total global terrestrial detrital carbon, indicating their importance to the global carbon cycle. In light of the dominance of *Sphagnum fuscum* in bogs and their large contribution to the annual accumulation of carbon in peatlands (Thormann et al. 1999b), it is surprising that little is known about the organisms inhabiting living and decomposing *S. fuscum* plants. It has been suggested that fungi are the principal decomposer microbes in many acidic ecosystems, such as bogs, and assume a more dominant role than bacteria (Latter et al. 1967, Williams and Crawford 1983). However, the majority of recent studies investigating carbon dynamics in peatlands concentrate on bacterial populations and their role in the mineralization of carbon to produce the greenhouse gas methane (CH_4) (Bubier et al. 1993, Roulet et al. 1993, Yavitt et al. 1993). Furthermore, some studies do not consider fungi as organisms involved in the decomposition, and hence mineralization, of plant litters altogether (Gilbert et al. 1998).

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[5] A version of this appendix has been submitted for publication: Thormann, M. N., R. S. Currah, and S. E. Bayley. The relative ability of fungi from *Sphagnum fuscum* to mineralize carbon. Canadian Journal of Microbiology.

To investigate the mycota associated with *Sphagnum fuscum*, fungi were isolated from living (May to September 1997) and decomposing (September 1997 to September 1999) *S. fuscum*. Among 262 isolates, zygomycetes, ascomycetes, and basidiomycetes were all represented, but for an initial assessment of their enzymatic abilities, I selected a single strain of each of five hyphomycetes, two teleomorphic ascomycetes, one zygomycete, and one basidiomycete. These included *Oidiodendron maius* Barron (ericoid mycorrhizal fungus) and *O. scytaloides* Gams & Söderström, an unusual species of *Acremonium* similar to *A. curvulum* W. Gams, two common soil and phylloplane species, *Penicillium thomii* Maire and *Trichoderma viride* Pers. *ex* S. F. Gray, two ascomycetes generally regarded as being coprophilous, *Sordaria fimicola* (Rob.) Ces. & de Not. and *Sporormiella intermedia* (Auersw.) Ahmed & Cain, the common zygomycete *Mucor hiemalis* Wehmer, and an unidentified basidiomycete. To determine their potential roles as carbon mineralizers and saprophytes of *S. fuscum*, their ability to utilize each of tannic acid, cellulose, and starch as a carbon source were examined. Relative *in vitro* mass losses of *S. fuscum* and spruce wood chips incurred by these nine taxa over a two-month period also were measured.

METHODS

Study area and site description

Mild summers and cold, snowy winters characterize the climate of southern boreal Alberta. The mean annual temperature is 1.7 °C and the total mean precipitation is approximately 500 mm (Environment Canada 1982). The Perryvale bog (54° 28' N, 113° 16' W) lies within the Subhumid Low Boreal ecoclimate region of Canada (Ecoregions Working Group 1989) and is dominated by *Picea mariana*, *Vaccinium vitis-idaea* L., *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Sphagnum fuscum*. A more detailed site description with respect to vegetation composition and surface water chemistry is in Thormann et al. (1999a) and Thormann et al. (2001).

The top 3 cm of approximately 20 individual living, healthy *Sphagnum fuscum* plants were collected in early May, early July, and early September 1997 and processed as outlined below. A decomposition study using nylon mesh bags (3 x 6 cm, 1 mm gauge) was initiated that fall (Thormann et al. 2001). Briefly, between five and eight individual fresh *S. fuscum* plants (top 3 cm) were placed into each of the decomposition bags and subsets of triplicate decomposition bags with decomposing *S. fuscum* were retrieved after 20 and 50 days in 1997, after eight and 12 months in May and September 1998, respectively, and after 20 and 24 months in May and September 1999, respectively.

Cultural techniques

Ten randomly selected, cleaned segments of *S. fuscum* were cut with a flame-sterilized scalpel into 10 to 12 smaller segments (approximately 5 x 5 mm in size). These were surface-sterilized for five minutes in 10% hydrogen peroxide (H_2O_2) and washed with sterilized, distilled water (d-H_2O). Five randomly selected *S. fuscum* segments were placed on each of three plates of Potato Dextrose Agar (PDA, 39.0 g Difco potato dextrose agar, 1.0 L d-H_2O), PDA with rose bengal (0.03%), PDA with benomyl (0.0002%), and Mycobiotic agar® (MYC, containing cycloheximide, 35.6 g Difco mycobiotic agar, 1.0 L d-H_2O). All media were amended with oxytetracycline (0.01%) to suppress bacterial growth. Plates were incubated at room temperature in the dark and fungi were sub-cultured onto Malt Extract Agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) as soon as they grew from the plant material. For identification purposes, slide cultures (Sigler 1993) on mixed cereal agar (Pablum®, H. J. Heinz Company of Canada Ltd., 100.0 g mixed cereal, 15.0 g Difco agar, 1.0 L d-H_2O) were prepared, mounted in polyvinyl alcohol, and photographed using an Olympus BX-50 microscope with a PM-10AK photosystem.

Representative cultures or slides were deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH) and/or the University of Alberta Cryptogamic Herbarium (ALTA) and/or the Centraalbureau voor Schimmelcultures (CBS).

Enzymatic degradation of selected carbon sources

Cellulose degradation was tested using the cellulose-azure method (Smith 1977) with modified Melin-Norkrans medium (MMN, 1.0 g d-glucose anhydrous, 2.0 g Difco malt extract agar, 1.0 g yeast extract, 10.0 g KH_2PO_4, 5.0 g $(NH_4)_2HPO_4$, 3.0 g $MgSO_4 \cdot 7H_2O$, 1.0 g $CaCl_2$, 0.5 g NaCl, 12.0 g Difco agar, and 1.0 L d-H_2O) substituted for the nutrient medium. Approximately 20 mL of MMN were added to 50 mL Pyrex culture tubes, these were autoclaved, and the medium was allowed to solidify. A 2% (w v^{-1}) cellulose-azure preparation in MMN was autoclaved separately and approximately 1.5-2.0 mL of the suspension was transferred into each Pyrex culture tube. For each species, three Pyrex culture tubes with cellulose-azure medium were inoculated with small plugs of mycelium and stored in the light at room temperature.

Degradation of cellulose was indicated by the release of the azure dye from the cellulose agar and its diffusion into the lower, clear layer of MMN.

The presence of polyphenol oxidases (PPO) was tested using tannic acid medium (TAM, 5.0 g Tannic acid [Baker analyzed], 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L d-H_2O) (Davidson et al. 1938). For each species, three petri plates of TAM were inoculated and stored in the dark at room temperature. A positive reaction was the formation of a dark brown pigment surrounding the point of inoculation, generally within four days after inoculation.

Starch degradation was tested by adding 2.0 g of soluble starch (BDH Chemicals Canada Ltd., Toronto) to 1.0 L MMN (Hutchison 1990). Once the individual colonies covered approximately 75% of the petri plates, they were flooded with an iodine solution (5.0 g KI, 1.5 g I, 100.0 mL d-H_2O). After five minutes, the solution was decanted and a clear zone around the colony in an otherwise purple plate indicated that amylase was produced and starch was degraded.

Visual comparative qualitative and quantitative evaluations ('+++', '++', '+', and '—' indicating decreasing quantities of degraded carbon source) were made based on the amount of azure dye released in the cellulose-azure assay and the amount of discoloration on the top and reverse of the TAM petri plates in the tannic acid assay. The width of the clear zone around colonies on the starch plates was used to assess the degree of amylase synthesis.

Cladosporium herbarum (Pers.) Link *ex* Gray, which is known to degrade cellulose (Marsh et al. 1949), tannic acid (Minoura and Okazaki 1968), and starch (Domsch 1960), was used as a positive control. This taxon was isolated from living *Sphagnum fuscum*, but was not used in the decomposition experiments.

Decomposition of *Sphagnum fuscum* plants and spruce wood chips

For each of the nine fungal taxa, 40 mL of peptone broth agar (20.0 g Difco agar, 1.0 g Difco bacto-peptone broth, 1.0 L d-H_2O) was poured into each of six 100 x 80 mm glass petri dishes. These dishes were inoculated with one of the nine fungal taxa. One 2.5 x 3.0 cm, 65 µm gauge polyester mesh pouch (to minimize plant material losses during handling) containing the top 3 cm of four *Sphagnum fuscum* plants was placed into each petri dish. Filled pouches were dried at 48 °C to constant weight, weighed to the nearest 0.01 g, and autoclaved at 121 °C (liquid cycle) for 15 minutes prior to placement into the petri dishes. After four and eight weeks, the pouches were removed from three petri dishes and fungal mycelium was carefully removed from the surface. The pouches were dried at 48 °C to constant weight, weighed to the nearest 0.01 g, and the mass loss was determined by subtracting the final mass from the initial mass for each pouch. Mass losses were expressed as percentages of the initial masses.

This experimental design was duplicated using ten 8 x 8 x 4 mm (approximate dimensions) spruce wood chips per petri dish instead of *Sphagnum fuscum*. The wood chips were autoclaved at 121 °C (liquid cycle) for 20 minutes prior to placing them directly onto the medium. Mass losses were determined as outlined above. Twelve petri dishes served as controls and were not inoculated with any fungi. Mass losses due to leaching of nutrients from the bryophyte litter and spruce wood chips were determined from these after four and eight weeks.

RESULTS

Fungi isolated from *Sphagnum fuscum*

Two hundred sixty-two isolates of fungi, representing 55 different species (Chapter 3), were derived from living and decomposing *Sphagnum fuscum* between May 1997 and September 1999. Of these, I selected nine species for the current study (Appendix 3 - Table 1): (1) *Sordaria fimicola*, with its broad, fusiform ascospores with a germ pore and gelatinous sheath; (2) *Sporormiella intermedia*, identified by its multiseptate, cylindrical ascospores with a gelatinous sheath; (3) *Oidiodendron scytaloides*, characterized by dematiaceous conidiophores with terminal, fertile hyphae that produce pale grey to brown arthroconidia and the formation of pale-brown chlamydospores singly or in short, compact chains; (4) *Oidiodendron maius*, with its tall conidiophores with terminal, undulating fertile hyphae and grey colonies; (5) *Acremonium cf. curvulum*, identified by its simple phialides that produce lightly to acutely curved hyaline conidia. My isolates differ from *A. curvulum* (Gams 1971) by their pale yellow to pale cream colony pigmentation, slow sporulation, scant aerial mycelium, and always simple phialides. Otherwise, cultural and morphological characteristics are identical; (6) *Penicillium thomii*, with its flesh to pink coloured robust sclerotia, simple monoverticillate conidiophores, and loose conidial columns, (7) *Trichoderma viride*, characterized by roughened, globose conidia originating from slender, irregularly-bent phialides on pyramidally-branched conidiophores; (8) *Mucor hiemalis*, identified by slightly sympodially branched sporangiophores, dark brown deliquescing sporangia, a globose to ellipsoidal columella, and ellipsoidal sporangiospores; and (9) an unidentified basidiomycete sp. characterized by white, patchy, aerial mycelium, hyaline, abundant, dry, arthroconidia of various shapes (rectangular, barrel-shaped, curved), a strong sweet odour, and clamp connections. None of these nine taxa has been reported previously from *S. fuscum*, although some of these species have been isolated previously from peat (McLennan and Ducker 1954, Thrower 1954, Christensen and Whittingham 1965, Dooley and Dickinson 1971, Dal Vesco 1974-75, Nilsson et al. 1992).

Enzymatic degradation of selected carbon sources and mass losses of *Sphagnum fuscum* plants and spruce wood chips

Distinct differences in the degradation of cellulose and tannic acid by these nine fungal taxa were apparent (Appendix 3 - Table 2). *Oidiodendron maius* and *Oidiodendron scytaloides* were the only two taxa that degraded tannic acid. However, most of the taxa degraded cellulose (eight of nine) and starch (seven of nine) effectively (Appendix 3 - Table 2).

Generally, mass losses of spruce wood chips exceeded those of *Sphagnum fuscum* ($p < 0.05$) (Appendix 3 - Table 3). Mean mass loss differences between these two substrates for the nine fungi combined after four and eight weeks of decomposition were 2.3 and 3.1%, respectively (Appendix 3 - Table 3). The basidiomycete sp. caused the greatest (10.2%), while *Oidiodendron scytaloides* caused the smallest (3.4%) mass loss of spruce wood chips after eight weeks (Appendix 3 - Table 3). *Sordaria fimicola* and *Mucor hiemalis* caused the greatest and smallest mass losses of *S. fuscum* after eight weeks (5.1 and 0.1%, respectively) (Appendix 3 - Table 3). The remaining fungal taxa caused intermediate mass losses (Appendix 3 - Table 3). Generally, mass losses of either substratum were similar after four and eight weeks of decomposition.

Leaching accounted for 1.6 and 2.0% mass losses from *Sphagnum fuscum* after four and eight weeks, respectively. Mass losses from leaching were 0.3 and 0.4% for the spruce wood chips after four and eight weeks. These mass losses were subtracted from the measured mass losses prior to statistical analyses.

DISCUSSION

Enzymatic degradation of tannic acid, cellulose, and starch

Seven of the nine fungi degraded starch (Appendix 3 - Table 2), indicating amylase synthesis. Several *Acremonium* species other than *A. cf. curvulum* synthesize amylase (Franz 1975) and this enzyme has been shown to be synthesized by *Trichoderma viride*, *Penicillium thomii*, and *Mucor hiemalis* previously (see Domsch et al. 1980).

Substantial differences in the degradation of cellulose and tannic acid by the nine fungi were apparent (Appendix 3 - Table 2). *Sordaria fimicola* utilized cellulose as a carbon source (Jefferys et al. 1953, Domsch 1960); however, cellulase synthesis among *Acremonium* species is variable. The cellulolytic capability of *Oidiodendron maius* has been suggested by Hambleton and Currah (1997), while the ability of *Sporormiella intermedia* and *Oidiodendron scytaloides* to degrade cellulose has not been reported previously. The cellulolytic abilities of *Trichoderma viride*, *Penicillium thomii*, and *Mucor hiemalis* have been shown in the past and my results concur (see Domsch et al. 1980).

Synthesis of polyphenol oxidases was found in both species of *Oidiodendron*, but not in the other species (Appendix 3 - Table 2). Lignin constitutes the primary structural polymer of woody plant species. It is also found in herbaceous plant species, where it increases the structural rigidity of cell walls. Lignin is a complex molecule, thus, the synthesis of polyphenol oxidases among fungi is less common compared to cellulases and amylases (Domsch et al. 1980). Utilization of lignin by *Oidiodendron* species has been demonstrated previously (Haselwandter et al..1990).

Enzymatic degradation of *Sphagnum fuscum* plants and spruce wood chips

Generally, mass losses of spruce wood chips exceeded those of *Sphagnum fuscum* over the first eight weeks of decomposition (Appendix 3 - Table 3). Concentrations of lignin or lignin-like substances and cellulose in gymnosperm wood (40-50% cellulose, 25-35% lignin) (Rayner and Boddy 1988) and *S. fuscum* (< 4.5% starch, 38% cellulose, 30% lignin-like substances) (Yavitt et al. 1997, Turetsky et al. 2000) are similar, therefore, it is surprising that their mass losses differed substantially. In decomposition studies, litter quality (tissue concentrations of nitrogen, phosphorus, phenolic and tannic compounds, lignin, cellulose, and hemicellulose) has been implicated to affect mass losses of herbaceous and woody plant litter (Clymo 1965, Johnson and Damman 1991, Kasai et al. 1995, Tsuneda and Thorn 1995, Szumigalski and Bayley 1996a, Thormann and Bayley 1997a; Thormann et al. 2001). For example, carbon to nitrogen (C:N) quotients of living and decomposing *S. fuscum* are generally < 100 (Szumigalski and Bayley 1996a, Thormann et al. 2001). Conversely, C:N quotients of wood are usually >1000 and can be as high as 2500 (Rayner and Boddy 1988), indicating significantly lower concentrations of nitrogen in wood. These differences should have contributed to lower decomposition rates for the wood chips compared to the bryophyte. Previous studies have shown that mass losses of woody plant tissues exceed those of bryophyte tissues after one year (Bartsch and Moore 1985, Szumigalski and Bayley 1996a). Johnson and Damman (1991, 1993) showed that inherent, physiological characteristics of *Sphagnum* tissues, such as the cell wall composition, controls the decay of this bryophyte in peatlands. The decay of wood has been ascribed primarily to basidiomycetes and it has been shown that some basidiomycetes have the ability to parasitize bacteria (Barron 1988) and yeasts (Hutchison and Barron 1990) or trap nematodes (Barron and Thorn 1987) to obtain nitrogen. Despite the high C:N quotient of wood compared to those of many other substrates, its decomposition rate may be similar to substrates with lower C:N quotients, such as *S. fuscum*, because some of the fungi primarily associated with wood decay have alternate strategies to obtain crucial elemental nutrients, such as nitrogen and phosphorus.

Peptone, a source of nitrogen, was added to the base medium in the glass petri dishes to assure growth of the fungi prior to colonization of the plant material. This nitrogen supply may have affected the growth rates of the fungi and their ability to colonize and ultimately degrade these two plant materials; however, alternative sources of nitrogen and other elemental nutrients are available to fungi *in situ*. Therefore, my base medium did not provide any sources of nutrients to these fungi that they would not have access to in nature. Furthermore, this study examined the relative mass losses of these two natural substrates incurred by nine fungi *in vitro*. Natural conditions differ significantly and results would likely be different. *In situ* mass losses of *S. fuscum* were 14 and 17% after four and eight weeks, respectively (Thormann et al. 2001). Not surprisingly, those mass losses substantially exceed the single-taxon *in vitro* mass losses reported here due to large and diverse microbial (fungi and bacteria) and invertebrate communities that combine to decompose plant materials in nature.

Autoclaving did not alter the morphology of the plant material (Tsuneda et al. 2001); however, the internal structure of the living, photosynthetically active cells likely changed during the sterilization process. Less invasive sterilization techniques, such as gamma-irradiation, may decrease the impact on the plant tissues.

Carbon mineralization by fungi

Northern peatlands store a significant portion of the world's terrestrial carbon as peat (Gorham 1990). With increasing atmospheric CO_2 concentrations and subsequent temperature increases, these peatlands may change from carbon sinks to carbon sources (Hilbert et al. 2000), whereby some of the stored carbon is mineralized and released as CO_2 (aerobic decomposition) or CH_4 (anaerobic decomposition). Most recent studies using carbon fluxes from peatlands as indicators of rates of decomposition concentrate on the production of CH_4 by bacterial populations (Bubier et al. 1993, Roulet et al. 1993, Yavitt et al. 1993), because CH_4 has a 7.5x higher global warming potential per molecule than CO_2 (Houghton 1997). Fungi generally are not addressed or are ignored altogether as important components of mineralization processes (Gilbert et al. 1998). However, in acidic ecosystems, such as bogs, fungi may assume a more dominant role than bacteria and the majority of cellulolytic organisms may be fungi (Latter et al. 1967). Furthermore, Williams and Crawford (1983) showed that fungi were more diverse in their abilities to utilize a variety of carbon sources and play an important role in the mineralization of lignin and cellulose in peatlands.

I obtained 262 fungal isolates from living and decomposing *Sphagnum fuscum*, the dominant hummock-forming bryophyte in northern peatlands (Vitt and Andrus 1977). Of these, I selected nine species, three from living, three from decomposing, and three from living and decomposing *S. fuscum*, in an effort to investigate their contribution to the decay of *S. fuscum* and ultimately the mineralization of carbon. These nine fungi had varying abilities to utilize different carbon sources (Appendix 3 - Table 2) and caused varying mass losses of *S. fuscum* and spruce wood chips *in vitro* (Appendix 3 - Table 3). My results suggest that these nine, and likely many other species isolated during this study, are involved in the decomposition of peat, and thus the mineralization of carbon, supporting results by Williams and Crawford (1983). Therefore, it is important to consider the roles of fungi in the mineralization of carbon, especially in northern peatlands with their significant carbon deposits.

Caution is required when interpreting these data, because they are only indications of the relative abilities of these nine fungi to degrade tannic acid, cellulose, and starch or cause mass losses of *Sphagnum fuscum* and spruce wood chips. These fungi compete for resources with other organisms *in situ*, *i.e.* in their realized niche, which may lead to the suppression of some of the abilities expressed *in vitro*, *i.e.* in their fundamental niche. The fundamental niche of an organism is always larger than its realized niche due to the absence of competition in the former. This study did not determine if these taxa have similar enzymatic abilities in the presence of other organisms or *in situ* and additional studies are needed to investigate these aspects. Furthermore, histological examinations of decomposed plant material are necessary to confirm and refine these results. Nonetheless, these data indicate that microfungi have considerable potential to mineralize carbon of bryophilous and lignicolous residues in bogs.

Roles of the nine fungi in natural habitats

Some *Oidiodendron* species, such as *Oidiodendron maius*, are mycorrhizal with members of the Ericaceae, such as *Rhododendron* and *Vaccinium* species common to peatlands (Barron 1962, Stoyke and Currah 1991, Hambleton and Currah 1997). The ability to degrade cellulose and tannic acid by *Oidiodendron* species may be necessary for the successful colonization of the root cortical cells of members of the Ericaceae. Tsuneda et al. (2001) showed that *O. maius* has the ability to degrade cell walls of *Sphagnum fuscum* by simultaneously degrading all cell wall components, such as amorphous cell wall components and microfibrillar elements. *Oidiodendron scytaloides* is common to soils of oak and coniferous forests in Europe (Gams and Söderström 1983), but it is less common in North America. Its enzymatic abilities have not been tested in the past; however, the presence of this fungus in roots of dying *Abies* sp. (Sigler & Flis 1998) and decomposing *S. fuscum* suggests that it is a saprophyte of plant materials and may have cellulolytic and lignolytic qualities, as supported by my data (Appendix 3 - Table 2).

The ascomycetes *Sordaria fimicola* and *Sporormiella intermedia* are classical coprophilous fungi that frequently have been isolated from herbivore and carnivore dung in the past (Iftikhar and Cain 1972, Lundqvist 1972). It has generally been assumed that coprophilous fungi are restricted to the dung of specific animals due to the complex nature of dung, caused by the age, kind, grade of decomposition, and chemical and physical properties of the dung of different animals (Lundqvist 1972). For example, *S. fimicola* grows preferentially on dung of herbivores (horses, hares, rabbits) (Lundqvist 1972), possibly due to the coarse nature of the cellulosic materials prevalent in the dung of these animals. This ascomycete was able to degrade cellulose effectively (Appendix 3 - Table 2) and previously was deemed a "cellulose-eater" by Dal Vesco et al. (1967). *Sordaria fimicola* has been isolated repeatedly from peat (McLennan and Ducker 1954, Thrower 1954) and may be more involved in the decay of plant residues than has been assumed previously. Many herbivorous animals, such as moose, deer, and rabbits, frequent bogs to forage on herbs, shrubs, and lichens. Thus, the spores of these coprophilous fungi may be consumed and dispersed by these herbivores, thereby meeting the suggested spore germination requirements (acidity) outlined by Bell (1983). Nonetheless, I suggest that some coprophilous fungi may have an alternate life strategy and can act as plant saprophytes under certain conditions. The pH of bogs is between 3.8 and 4.1 (Szumigalski and Bayley 1996b, Thormann and Bayley 1997b, Thormann et al. 2001) and may be low enough to induce germination of the ascospores. I isolated both ascomycetes from living *Sphagnum fuscum* in July 1997, indicating that they may be saprophytic on plants following the germination of the discharged ascospores on nearby plants or peat and prior to consumption by herbivores, a theory first suggested by Webster (1970).

Acremonium cf. curvulum is strongly cellulolytic but not lignolytic (Appendix 3 - Table 2) and has been isolated principally from soils and leaves of plants (Gams 1971). I isolated this species from several decomposing *Sphagnum fuscum* segments in 1998. *Acremonium curvulum* is uncommon in continental North America (previously isolated from soils in Minnesota, U.S.A., and Ontario, Canada) (CBS databases). My isolate may be an important cellulose degrader of *S. fuscum* in this bog, as indicated by the mass losses of *S. fuscum* incurred over the first eight weeks of decomposition (Appendix 3 - Table 3). This species degrades cell wall components of *S. fuscum* in a preferential mode, first by fragmenting and removing the amorphous outer cell wall layer and then attacking the microfibrils of the central cell wall layer, thereby producing voids within the leaf tissues (Tsuneda et al. 2001). Many *Acremonium* species occur in soils and plant materials worldwide and their role as saprophytes have been suggested previously (Gams 1971). Gams (1971) indicated that only a few *Acremonium* species are saprophytes or parasites of specific plant species, whereas the majority are generalists and can be isolated from a variety of substrates. Both of my isolates came from a cycloheximide-amended medium, indicating *A. cf. curvulum*'s resistance to this growth inhibitor.

The basidiomycete sp. caused the greatest mass losses of the spruce wood chips (10.2%) (Appendix 3 - Table 3), despite a limited enzymatic profile (Appendix 3 - Table 2). Many basidiomycetes are efficient wood saprophytes and contribute to nutrient cycling within ecosystems (Lumley et al. 2001). My isolates shared some morphological characteristics, such as arthroconidial and hyphal morphology and colony characteristics, with some of these, *e.g. Bjerkandera adusta* (Willd. *ex* Fr.) P. Karst. (Stalpers 1978). *Bjerkandera adusta* occurs primarily on angiosperms and is less commonly isolated from conifers, such as species of *Picea* (Stalpers 1978). Although I did not isolate fungi from spruce wood, black spruce (*Picea mariana*) is common to western continental bogs and the presence of this basidiomycete in my bog would not be unusual. Conversely, my basidiomycete isolates also were similar to the mycoparasite *Geotrichopsis mycoparasitica* Tzean & Estey (Tzean and Estey 1991). This mycoparasite has been shown to parasitize a variety of hyphomycetes (Tzean and Estey 1992), including some that were isolated during my investigation of the filamentous microfungus communities of living and decomposing *S. fuscum*. More extensive cultural, physiological, and /or molecular techniques are necessary to identify my basidiomycete isolates.

Penicillium thomii and *Trichoderma viride* are frequently isolated from a variety of living and decomposing organic substrates (see Domsch et al. 1980). Both taxa utilize cellulose and starch as carbon sources (Appendix 3 - Table 2) and are thought to cause the largest mass losses of decomposing plant litters by mineralizing cellulose and hemicellulose (Deacon 1984). Although generally isolated from the surfaces of plant materials, they have the ability to invade and colonize deeper plant tissues and play significant roles in the degradation of organic materials. Furthermore, *T. viride* is a mycoparasite and has the ability to decrease interspecific competition for nutrients by parasitizing other fungi within the same substrate.

Mucor hiemalis is one of the most common soil fungi and the most frequent representative of the Mucorales (Domsch et al. 1980). It has a worldwide distribution and has been isolated from a variety of habitats, including peatlands (McLennan and Ducker 1954, Thrower 1954). It is considered a "sugar fungus", readily utilizing simple organic materials that leach naturally out of plant materials (Deacon 1984). Leaching accounted for mass losses of up to 2% from *S. fuscum* and spruce wood chips.

CONCLUSIONS

In an ongoing comprehensive survey of fungi associated with living and decaying *Sphagnum fuscum*, nine fungal taxa were isolated that represent new records for fungi on *Sphagnum* species. These were *Sordaria fimicola*, *Sporormiella intermedia*, *Acremonium cf. curvulum*, *Oidiodendron maius*, *Oidiodendron scytaloides*, *Penicillium thomii*, *Trichoderma viride*, *Mucor hiemalis*, and one unidentified basidiomycete, each with specific abilities to utilize tannic acid, cellulose, and starch as carbon sources. Their varying abilities to degrade *S. fuscum* and spruce wood chips paralleled those from the pure carbon sources and indicate the diverse enzymatic abilities of the fungi involved in the decomposition of plant litters. The presence of the two ascomycetes, both species of *Oidiodendron*, and *A. cf. curvulum* in *S. fuscum* suggests that they play important roles in the decay of *S. fuscum* and the mineralization of carbon in peatlands.

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Appendix 3 - Table 1. Accession numbers and isolation information of the nine fungal taxa isolated from living and decomposing *Sphagnum fuscum* from a bog in southern boreal Alberta, Canada.

	Isolation information	
Fungi (accession numbers)	Substrates (numbers of isolates)	Media
Acremonium cf. curvulum (CBS 102853)	decomposing (3) *S. fuscum*	MA
Basidiomycete sp. (ALTA 10853)	living (3) *S. fuscum*	PDA, PDA plus benomyl
Mucor hiemalis (ALTA 10697)	living (10) and decomposing (26) *S. fuscum*	PDA, PDA plus benomyl, PDA plus rose bengal
Oidiodendron maius (ALTA 10700, UAMH 9749)	decomposing (1) *S. fuscum*	PDA
Oidiodendron scytaloides (UAMH 9750)	living (2) and decomposing (1) *S. fuscum*	MA
Penicillium thomii (ALTA 10860)	living (4) and decomposing (19) *S. fuscum*	PDA, PDA plus benomyl, PDA plus rose bengal, MA
Sordaria fimicola (ALTA 10705, UAMH 9475)	living (4) *S. fuscum*	PDA, PDA plus rose bengal
Sporormiella intermedia (ALTA 10706)	living (1) *S. fuscum*	PDA plus rose bengal
Trichoderma viride (ALTA 10713)	living (4) and decomposing (12) *S. fuscum*	PDA, PDA plus benomyl, PDA plus rose bengal, MA

Note: ALTA = University of Alberta Cryptogamic Herbarium, CBS = Centraalbureau voor Schimmelcultures, and UAMH = University of Alberta Microfungus Collection and Herbarium. PDA = potato dextrose agar, MA = mycobiotic agar.

Appendix 3 - Table 2. Enzymatic degradation of tannic acid, cellulose, and starch by nine fungal taxa isolated from living and decomposing *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada.

Fungal taxa	Tannic acid	Cellulose	Starch
Acremonium cf. curvulum	---	+++	++
Basidiomycete sp.	---	++	---
Mucor hiemalis	---	+	+++
Oidiodendron maius	+++	+	+
Oidiodendron scytaloides	+	++	++
Penicillium thomii	---	++	+++
Sordaria fimicola	---	+	---
Sporormiella intermedia	---	---	+
Trichoderma viride	---	+++	+++

Note: '+++' = strong reaction, '++' = intermediate reaction, '+' = weak reaction, '---' = no reaction. n = 3 per treatment.

Appendix 3 - Table 3. Mass losses of spruce wood chips and *Sphagnum fuscum* plants by nine fungal taxa from living and decomposing *S. fuscum* from a bog in southern boreal Alberta.

Fungal taxa	Substrata	Mass losses (% ± SE)	
		Four weeks	Eight weeks
Acremonium cf. curvulum	Spruce wood chips	4.5 (0.6) *a1*	4.6 (0.1) *a1*
	S. fuscum *	3.3 (0.4) *a1*	3.9 (0.8) *a1*
Basidiomycete sp.	Spruce wood chips	4.8 (0.3) *a1*	10.2 (1.1) *b1*
	S. fuscum	1.6 (0.6) *a2*	1.7 (0.7) *a2*
Mucor hiemalis	Spruce wood chips	4.3 (0.2) *a1*	4.9 (0.2) *b1*
	S. fuscum	0.3 (0.0) *a2*	0.1 (0.0) *a2*
Oidiodendron maius	Spruce wood chips	4.4 (0.2) *a1*	4.6 (0.2) *a1*
	S. fuscum	1.5 (0.4) *a2*	2.5 (0.5) *a2*
Oidiodendron scytaloides	Spruce wood chips	3.3 (0.1) *a1*	3.4 (0.5) *a1*
	S. fuscum	3.2 (0.3) *a1*	3.6 (1.2) *a1*
Penicillium thomii	Spruce wood chips	4.2 (0.3) *a1*	5.1 (0.3) *b1*
	S. fuscum	0.5 (0.1) *a2*	1.8 (0.2) *b2*
Sordaria fimicola	Spruce wood chips	5.2 (0.3) *a1*	5.2 (0.6) *a1*
	S. fuscum	4.2 (1.2) *a1*	5.1 (0.7) *a1*
Sporormiella intermedia	Spruce wood chips	3.5 (0.3) *a1*	5.1 (0.3) *b1*
	S. fuscum	3.4 (0.4) *a1*	3.2 (0.3) *a2*
Trichoderma viride	Spruce wood chips	4.3 (0.1) *a1*	5.6 (0.2) *b1*
	S. fuscum	0.4 (0.0) *a2*	0.5 (0.0) *a2*

* *In situ* mass losses of *S. fuscum* were 14 and 17% after four and eight weeks, respectively (Thormann et al. 2001). Italic letters indicate significant differences in mass losses between decomposition periods for each substratum, while italic numbers indicate significant differences in mass losses between the substrata at each decomposition period for each fungal taxon. n = 3 per treatment.

Appendix 4. Accession numbers of microfungi isolated from living and decomposing *Sphagnum fuscum* from a bog and *Carex aquatilis* leaves and rhizomes and *Salix* planifolia leaves and roots from a fen in southern boreal Alberta, Canada.

Fungal species	Coll. Number	ALTA	UAMH	CBS
Acremonium butyri	MNT-78	11710	---	---
A. chrysogenum	MNT-19	10669	---	---
A. cf. curvulum	MNT-5	---	9938	102853
A. egyptiacum	MNT-75	11711	---	---
Acremonium state of *Nectria rishbethii*	MNT-76	11714	---	---
A. strictum	MNT-21	10670	---	---
Alternaria alternata	MNT-17	10671	---	---
Armillaria sinapina	MNT-65	---	9792	---
Arthrinium state of *Apiospora montagnei*	MNT-16	10672	---	---
Aspergillus niger	MNT-25	10673	---	---
A. versicolor	MNT-26	10674	---	---
Aureobasidium pullulans	MNT-24	10675	---	---
Basidiomycete sp. 1	MNT-52	10853	---	---
Basidiomycete sp. 2	MNT-53	10854	---	---
Basidiomycete sp. 3	MNT-66	11312	---	---
Basidiomycete sp. 4	MNT-67	11313	---	---
Basidiomycete sp. 5	MNT-68	11314	---	---
Basidiomycete sp. 6	MNT-69	11315	---	---
Basidiomycete sp. 7	MNT-70	11316	---	---
Basidiomycete sp. 8	MNT-71	11317	---	---
Bjerkandera adusta	MNT-80	11712	---	---
Botrytis cinerea	MNT-23	10676	---	---
Cladosporium cladosporioides	MNT-22	10677	---	---
C. herbarum	MNT-28	10678	---	---
C. murorum	MNT-93	12285	---	---
Dimorphospora foliicola	MNT-74	11713	---	---
Epicoccum purpurascens	MNT-2	10679	---	---
Fusarium aquaeductuum var. *medium*	MNT-4	10680	---	---
F. chlamydosporum	MNT-12	10681	---	---
F. oxysporum	MNT-11	10682	---	---
F. sporotrichioides	MNT-10	10683	---	---
Hormonema dematioides	MNT-7	10684	---	---
Kernia retardata	MNT-64	---	9613	---
Monocillium constrictum	MNT-8	10685	---	---
M. nordinii	MNT-95	12286	---	---

Fungal species	Coll. Number	ALTA	UAMH	CBS
Mortierella alpina	MNT-31	10686	---	---
M. elongata	MNT-32	10687	---	---
M. ericetorum	MNT-33	10688	---	---
M. horticola	MNT-37	10691	---	---
M. humilis	MNT-38	10692	---	---
M. isabellina	MNT-39	10689	---	---
M. minutissima	MNT-42	10690	---	---
M. ramanniana var. *angulispora*	MNT-48	10693	---	---
M. ramanniana var. *ramanniana*	MNT-47	10694	---	---
M. renispora	MNT-41	10695	---	---
M. verticillata	MNT-40	10696	---	---
Mucor hiemalis	MNT-49	10697	---	---
Nodulisporium sp.	MNT-9	10698	---	---
Oidiodendron maius	MNT-1	10700	9749	---
O. scytaloides	MNT-13	10699	9750, 9751	---
Paecilomyces marquandii	MNT-55	10855	---	---
Penicillium chrysogenum	MNT-92	12288	---	---
P. funiculosum	MNT-56	10856	---	---
P. montanense	MNT-58	10858	---	---
P. odoratum	MNT-57	10857	---	---
P. purpurogenum	MNT-59	10859	---	---
P. thomii	MNT-60	10860	---	---
Phialocephala dimorphospora	MNT-51	10701, 10861	---	---
P. fortinii	MNT-14	10702	---	---
Polyscytalum cf. hareae	MNT-54	10862	---	---
Phialophora alba	MNT-73	11715	---	---
Phialophora cf. alba	MNT-94	12287	9929	---
P. cyclaminis	MNT-72	11716	---	---
P. malorum	MNT-77	11717	9862	---
P. melinii	MNT-79	11718	---	---
Pycnidial sp. 1	MNT-83	12289	---	---
Pycnidial sp. 2	MNT-84	12290	---	---
Pycnidial sp. 3	MNT-85	12291	---	---
Pycnidial sp. 4	MNT-86	12292	---	---
Pycnidial sp. 5	MNT-97	12293	---	---
Pycnidial sp. 6	MNT-88	12294	---	---
Pycnidial sp. 7	MNT-89	12295	---	---
Scopulariopsis brevicaulis	MNT-15	10704	---	---
Scopulariopsis state of *Kernia retardata*	MNT-18	10703	---	---
Sordaria fimicola	MNT-6	10705	9475	---
Sporormiella intermedia	MNT-3	10706	---	---

Fungal species	Coll. Number	ALTA	UAMH	CBS
Sporothrix state of *Ophiostoma stenoceras*	MNT-63	11311	9753	---
Sporothrix sp. 1	MNT-62	---	9752	---
Sporothrix sp. 2	MNT-91	12296	9930	---
Stagonospora caricis	MNT-81	12297	---	---
Stagonospora sp.	MNT-82	12298	---	---
Trichoderma aureoviride	MNT-35	10707	---	---
T. harzianum	MNT-34	10708	---	---
T. koningii	MNT-46	10709	---	---
T. piluliferum	MNT-44	10711	---	---
T. polysporum	MNT-45	10712	---	---
T. pseudokoningii	MNT-43	10710	---	---
T. viride	MNT-36	10713	---	---
Ulocladium botrytis	MNT-20	10714	---	---
Verticillium balanoides	MNT-90	12299	9931	---
V. bulbillosum	MNT-30	10715	---	---
V. cephalosporium	MNT-29	10716	---	---
V. lecanii	MNT-50	10717	---	---
V. psalliotae	MNT-27	10718	---	---

Note: Coll. Number = collection number, ALTA = University of Alberta Cryptogamic Herbarium, UAMH = University of Alberta Microfungus Collection and Herbarium, CBS = Centraalbureau voor Schimmelcultures.

APPENDIX 5. GLOSSARY OF MYCOLOGICAL TERMS

This glossary includes mycological terminology used in this thesis as well as terminology that does not appear in this thesis but may be of interest to non-mycologists. This glossary is based on Currah (2001) with modified definitions from Hawksworth et al. (1995).

acerose - needle-like and stiff, like a pine needle.

acervulus (**-i**, pl.) - a saucer-shaped fructification produced by some Coelomycetes; supports conidiophores and may have various types of hairs along the margin; characteristic of the "Melanconiales".

acropetal conidiogenesis - conidia form at the top or distal end of the conidial chain, see *Cladosporium*.

acropleurogenous - formed at the ends and at the sides, *e.g.* spores on a conidiophore.

adventitious septum - a septum that cuts off various parts of the protoplast and forms independent of nuclear division.

aeciospore - dikaryotic spores formed mitotically in chains and in an aecium on a vascular plant host; constituting one of the possible five spore states ("I") in the rust fungi (Uredinales).

aecium (**-ia**, pl.) - a discrete structure on a plant infected with a rust fungus where aeciospores are produced.

agaric - a general term referring to a gilled mushroom.

aleuroconidium (**-ia**, pl.) - a single-celled terminal conidium.

ammonia fungi - taxa that increase in number when nitrogen levels are high. Also called proteophilous fungi.

ampulliform - flask-like in form.

amyloid - a reaction to Melzer's reagent that gives a purplish or bluish colour when starch (amylose) is present. See also dextrinoid and Melzer's reagent.

anamorph - a morphologically distinctive phase in the life cycle of a fungus; produces asexual propagules (conidia, sclerotia, bulbils, etc.).

anastomosis - fusion of adjacent hyphal branches.

anemophilous (adj.) - describes an organism or structure that is adapted to dispersal by air currents.

annellide - a type of phialide which, during conidium formation, leaves a ring of wall material at the apex of the sporogenous cell; recognized by parallel or rings of wall material at the phialide apex; *e.g. Scopulariopsis*.

annulus (**-i**, pl.) - also called a "ring"; remains of the partial veil which adheres to the stipe (or stalk) of a stipitate mushroom.

antheridium (**-ia**, pl.) - a cell that donates a nucleus during sexual reproduction.

apiculate - having an apiculus.

apiculus (**-i**, pl.) - a small pointed projection at the proximal end of a spore and indicating the sterigmatal end of the spore.

apophysis - swelling at the end of a sporangiophore, subtending the sporangium, in some species of the Mucorales.

apothecium (**-ia**, pl.) - a cup- or disc-shaped ascocarp.

arthroconidia - asexual spores arising from the conversion of a pre-existing hypha to a train of propagules; disarticulating at maturity.

ascocarp - any fruitbody of an ascomycete in or on which asci are formed.

ascogonial coil - a ring or coil-shaped cell which accepts nuclei or at least gives rise to asci.

ascogonial papilla (**-ae**, pl.) - the initial protuberance from the ascogonial coil which elongate and produce croziers.

ascospore - spore resulting from meiosis and enclosed within an ascus when mature.

ascostroma - a complex ascocarp in which ascosporogenesis occurs in one or more cavities within a stroma.

ascus (**-i**, pl.) - a sac-like cell in which ascospores develop after karyogamy and meiosis.

asteroseta (**-ae**, pl.) - star-shaped sterile element in the basidiocarps of some Aphyllophorales.

autoecious (adj.) - describing a fungus which requires only one host for the normal completion of the life cycle; a term used when describing the rust fungi, *cf.* heteroecious.

axenic - literally "without strangers"; a pure culture of an organism.

axoneme - the central core of microtubules in a flagellum, 9+2 configuration

baiting - the addition of special materials (*e.g.* cellulose, keratin, chitin) to a soil or water sample to encourage the growth of fungi which are substrate-specialists.

ballistospore - a spore, such as a basidiospore, that is forcibly ejected from the parent cell.

basal body - see kinetosome.

basidiocarp - the (meiosporic) fruit body of a basidiomycete.

basidiole - a sterile element resembling a basidium in the hymenium of basidiomycetes.

basidioma - = basidiocarp.

basidiospore - a haploid spore formed by meiosis on a basidium.

basidium - a terminal cell in which karyogamy and meiosis occur in basidiomycetes; often arranged to form a hymenium.

basipetal conidiogenesis - a pattern of asexual formation, in which the spores or conidia form from a fixed sporogenous locus, as for example in a phialide. The oldest condium is at the tip of the chain. See also "acropetal conidiogenesis".

basitonously - at the base, *e.g.* branching pattern of a sporangiophore.

biguttulate - having two oil drops (guttules) in a spore.

binding hyphae - thick-walled hyphae that are usually irregular in shape and branching; thought to bind together the hyphae comprising some basidiocarps.

biotroph - an organism capable of extracting nutrients from another organism without killing it; a haustorial parasite.

bitunicate - describing an ascus with two distinct wall layers.

biverticillate - having branching at two levels, *i.e.* having metulae bearing phialides, *e.g.* *Penicillium*.

blastic conidiogenesis - the process in which conidia form by cytoplasm being blown out from a fixed conidiogenous locus.

blastoconidia - a blastic conidium.

box-car formation - a term describing the appearance of fungal chromosomes as they are pulled to opposite poles of the cell during cell division.

brown rot - a type of wood decay in which the cellulosic fraction is removed from the cell walls, leaving the amorphous brown lignins.

capillitium (**-ia**, pl.) - a collective term for the network of sterile thread-like cells supporting the spores in gastermycetes and myxomycetes.

catenate - in chains.

cellulolytic fungi - fungi that can break down cellulose as a source of carbon and energy.

centrum - the contents of the ascocarp.

cephalodium (**-ia**, pl.) - a dot-like aggregation of cyanobacteria that occurs on the surface of some lichens.

chiastobasidium (**-ia**, pl.) - a basidium in which nuclear division occurs perpendicular to the long axis of the basidium, *cf.* stichobasidium.

chitin - a polymer of N-acetyl glucosamine and a distinctive component of the fungal cell wall.

chitinolytic - able to degrade chitin.

chitosan - a form of chitin found in the cell walls of zygomycetes and differing from chitin in having fewer acetyl groups.

chitosome - a type of vesicle containing chitin synthetase.

chytrid - a general label referring to any of the fungi that produce flagellated cells.

chlamydospore - a thick-walled, asexual resting spore.

cladistic analysis - a philosophical approach to the delimition of species and higher taxa that reflects their evolutionary history.

clamp connection - a buckle-shaped knob over the septum of some basidiomycetes representing a short hypha through which a nucleus migrated during mitotic division and extension of the tip cell.

cleistothecium (**-ia**, pl.) - a closed peridium found in some groups of ascomycetes.

coenocytic - multinucleate and usually lacking cross-walls.

coelomycete - fungus producing mitospores in pycnidia or acervuli.

collarette – a cup-shaped structure at the apex of a conidiogenous cell.

columella - a supportive and nurturing balloon-shaped structure that develops beneath the spores inside a sporangium, *e.g.* in zygomycetes.

conidiiferous - bearing conidia.

conidium (**-ia**, pl.) - asexual spore; also called mitospore.

conidiogenous cell - a cell giving rise to conidia.

conidiophore - a structure bearing conidia and/or conidiogenous cells.

convergent character - a common feature expressed by two unrelated organisms. A convergent character usually arises in response to similar ecological demands on two or more organisms.

coprophilous (adj.) - describes organisms that are found principally on dung.

corticolous - growing on bark.

cortina - the hairy, partial veil in the Cortinariaceae.

crozier - a hook formed during the formation of an ascus; homologous with a clamp connection.

cystidium (**-ia**, pl.) - a large and distinctive sterile element in the hymenium of basidiomycetes.

deliquescent - dissolving.

dematiaceous (adj.) - a term describing the darkly-pigmented or melanized cell walls of some fungi, *e.g. Cladosporium.*

dermatophyte - a fungus (usually a species of *Trichophyton* or *Microsporum*) that grows on/in the dermis of vertebrates where it causes disease.

dextrinoid - a reaction to Melzer's reagent that gives a red colour, *cf.* amyloid and Melzer's reagent.

dimitic (adj.) - refers to two types of hyphae (generative + binding or skeletal) being present in a basidiocarp.

dimorphic - having two morphologically distinct forms, such as a yeast phase and a hyphal phase.

discomycete - general and non-taxonomic term that refers to the apothecium-forming ascomycetes.

dolipore septum - a characteristic type of cross-wall between adjacent cells of the hyphae of dikaryotic basidiomycetes; the septal pore is bordered by a pronounced thickening on each face of the septum. Parenthesomes or septal pore caps enclose the opening on either side.

echinulate - having sharply-pointed spines.

ectal excipulum (**-a**, pl.) - outer tissue layer of an apothecium.

ectendomycorrhiza (**-as**, pl.) - fungi form distinctive hyphal structures inside and outside the cells of the root, *e.g.* mycorrhizas formed with conifers by *Wilcoxina* and *Hymenoscyphus.*

ectotrophic (adj.) - usually describes plants which rely on ectomycorrhizas to augment their mineral nutrition.

ectomycorrhiza (**-as**, pl.) - a type of mycorrhiza in which the cells of the mycobiont surround the cells of the root cortex of the host plant and usually form a coating (or mantle) on the root surface.

effused-reflexed - usually refers to a type of basidiocarp in the Aphyllophorales in which the hymenium-bearing tissue is partly lying flat against the surface of a stick or log and partly borne on the undersurface of a pileus.

endobiotic chytrid - a type of chytrid in which the sporangium develops within the host cell.

endocyclic - a type of rust in which the aeciospores can function as teliospores.

endomycorrhiza (**-as**, pl.)- the fungal cells develop within the cells of the root as in ericoid, VAM, and orchid mycorrhizas.

endophyte - a fungus living inside the organs (roots, stems, leaves, etc.) of a living plant.

endotunica - the inner layer of the ascus wall.

enveloping membrane system (EMS) - ascus vesicle; the pair of membranes, one inside the other, that delimit the developing ascospores. Wall material is deposited between the membranes. The inner membrane becomes the new plasma membrane of the ascospore cell.

epibiotic chytrid - a type of chytrid in which the sporangium develops on the surface of the host cell.

epigeous - forming on the surface of the ground (rather than below it).

epithecium - a layer covering the hymenium in discomycetes, composed of the swollen apices of paraphyses.

epixylous - on wood.

ergosterol - a sterol found in the plasma membrane of fungal cells. Sometimes used as an indirect method of assessing fungal biomass.

ergot - a term that refers to a fungal disease of grasses caused by species in the ascomycete genus *Claviceps*. The ovary is infiltrated with fungal tissue and swells to form a sclerotium. The term "ergot" can refer to the disease, the sclerotium, or the fungus.

ericoid mycorrhiza (-as, pl.) - an endomycorrhizal form that develops only in association with some groups within the Ericales. The mycobionts are inoperculate ascomycetes.

eucarpic chytrid - part of the thallus is specialized to produce zoospores, while other parts have an assimilative function.

eukaryote - an organism whose cell or cells contain a double-membrane bound nucleus and usually mitochondria.

excipulum (-a, pl.) - the sterile tissue making up the outer wall of a cupulate ascocarp.

exit papilla - the pore through which zoospores exit a zoosporangium.

fairy ring - a circle or arc of mushrooms (or dead grass in the absence of mushrooms) that indicate the margin of an expanding mycelium.

falcate - curved like the blade of a sickle.

fenestrate - having a series of perforations.

fimbria (-ae, pl.) - proteinaceous fibrils extending from the walls of some fungal cells and functioning in cell recognition.

folicolous - on leaves.

foliose thallus - a leaf-like thallus of a lichen.

fruticose thallus - a shrubby growth form in a lichen; can be erect or pendent.

funiculus - the cord at the base of a peridiole in the bird's nest fungi.

fusiform - spindle-like, narrowing towards the ends.

fusiform funiculus - the cord at the base of a peridiole in the bird's nest fungi.

gametangia - cells in which gametes are produced.

gasteromycete - basidiomycete which produce basidiospores within a peridium; basidiospores are statismospores and are not forcibly ejected. These fungi constitute a series of fungi with a common form but are not necessarily related by descent.

gasteromycetation - the evolutionary process whereby a fungus loses active meiospore release, instead retaining the sexually produces spores within a cavity surrounded by a wall or peridium. Concomitant with gasteromycetation is the evolution of elaborate mechanisms, often involving animals, which facilitate meiospore release and dispersal.

gelatinolytic - able to degrade gelatin.

germ tube - the hypha that emerges from the spore on germination.

generative hypha (-ae, pl.) - thin-walled hyphae which usually stain clearly with a vital stain; these hyphae give rise to skeletal and generative hyphae.

geosmin - a strong earthy odour produced by actinomycetes.

gleba - a mass of meiosporic tissue within the peridium of a puffball.

gloeopleurous hyphae - thin-walled, refractive hyphae that stain with vital stains in some basidiocarps.

guttulate - having oil drops (guttules) in a spore.

hamathecium (-ia, pl.) - a general term referring to sterile elements that form among the hymenial tissues except the asci. Thus, it would include paraphyses, paraphysoids, pseudoparaphyses, and periphysoids.

hapteron - a sticky pad or adhesive device produced as part of the dispersal phase in some fungi.

Hartig net - in an ectomycorrhizal root in cross-section, the pattern of hyphae between the epidermal and cortical cells forms a reticulum or "net". The structure is named after the German phytopathologist Heinrich Julius Adolph Robert Hartig, who was a professor of Botany in Munich.

haustorium (-ia, pl.) - a balloon or glove-shaped structure produced by a parasite that intrudes into the host cell through the cell wall and invaginates the plasma membrane increasing the surface area for the absorption of materials from the parasitized cell.

heteroecious - requiring two hosts to complete the life cycle; a common feature in some groups of rusts.

heterokaryon - a fungus with at least two genetically distinct nuclei per cell, sometimes following anastomosis.

heterothallic - a fungus which cannot breed with itself and requires another genetically distinct individual in order for a compatible cross to become established.

heteroxenous - having more than one host.

hilum - a mark or scar, especially that on a spore at the point of attachment to a conidiogenous cell or sterigma.

hoary - covered with silky hairs.

holocarpic - all of the fruit body is converted to spores or spore producing cells.

holomorph - a concept embodying the entire life cycle of a fungus with all of its reproductive and vegetative states.

homoiomerous - refers to lichen thalli with fungal and algal cells mixed evenly throughout the tissue, *e.g. Collema.*

homokaryon - having genetically identical nuclei.

homothallic - sexual reproduction can occur between genetically identical nuclei.

Hülle cells - terminal and intercalary thick-walled cells that form in association with ascomata of some Plectomycetes, particularly in the Trichocomaceae.

hyaline - transparent or colourless.

hygroscopic - responding to an increase in moisture by softening or opening up, as in some sporocarps.

hymenium - a layer of tissue giving rise to meiospores.

hymenomycetes - basidiomycetes that produce basidia in a hymenial layer.

hypha (-ae, pl.) - a tubular structure in which a rigid wall encloses a protoplast or series of protoplasts; extending by tip growth. The fundamental structural unit of most fungi.

hyphal analysis - the teasing apart of tissues of the sporocarps of macrofungi to determine the component cells types.

hyphidia - sterile hyphal structures in the hymenium of basidiomycetes.

Hyphomycetes - a "form-class" of mitosporic or vegetatively reproducing fungi in which conidia (if formed) are entirely exposed at maturity. Includes four morphological groups: Agonomycetales (or *mycelia sterilia*), Hyphomycetales (majority of molds), Stilbellales (conidiogenous cells aggregated to form synnemata), and Tuberculariales (conidia formed on cushion-shaped aggregations of conidiogenous cells).

hypochnoid - describes a dry, diffuse, resupinate sporocarp, *e.g. Tomentella*.

hypogeous - forming below the surface of the soil.

hypogeous fungus - fungus that forms sporocarps beneath the surface of the soil.

hypothecium (**-ia**, pl.) - medullary excipulum tissue that underlies the hymenium in discomycetes.

hysterothecium (**-ia**, pl.) - an elongated ascocarp with a slit-like opening.

incertae sedis - uncertain taxonomic position.

Ingoldian fungi - aquatic fungi which have spores with elongate arms, *e.g.* tetraradiate conidia.

ingroup - the putatively monophyletic group of closely related species or taxa in a phylogenetic study.

inoperculate - refers to the dehiscence mechanism of an ascus that releases ascospores through a pore or a slit rather than through a opening covered with a lid or operculum.

isidium (**-ia**, pl.) - a vegetative protuberance from a lichen thallus containing algal cells. Isidia can break off and disperse the lichen to new habitats.

ixocutis - a slimy cuticle.

killer yeasts - produce proteinaceous toxins that kill closely related forms.

kinetosome - a body at the base of a flagellum made up of a cylinder of 9 triplets of microtubules. Also called a basal body.

koji - rice inoculated with *Aspergillus oryzae* and used as a source of sugars and flavours for various fermented products in Japanese foods, beverages, and condiments, *e.g.* miso, sake, and soya sauce.

laccate - polished, shiny.

lamella (**-ae**, pl.) - vertical plate of tissue supporting the hymenium of agarics.

lecanorine - in lichens, an apothecium with a well-defined ("thalline") excipulum of tissue made up of both the alga and fungus, *e.g. Parmelia*.

lecideine - in lichens, an apothecium in which the excipulum is made up of only fungal cells.

lentic - found in still or stagnant water.

lenticular - like a double-convex lens in form

lichen - the symbiotic arrangement between a fungus and an alga which is so closely integrated that it looks and behaves as a unique, individual organism.

lignicolous - living in or on wood.

lignolytic fungi - fungi with the ability to break down polyphenolic polymers found in wood.

limoniform - lemon-like in form

locule - cavity.

lotic - found in running water.

macrocyclic rust - all five spore-producing stages of the rust life cycle are present in this type of rust.

macromycetes - fungi with large sporocarps easily observed with the naked eye, *e.g.* mushrooms, puffballs, cup fungi, morels, truffles, etc.

macronematous - a conidiophore filament that is clearly different from the vegetative hypha. (*cf.* micronematous).

maculate - with spots or blotches.

mannitol - a sugar alcohol storage compound found in fungal tissues, especially in lichens and mycorrhizas.

mantle - a coat of fungal tissue as surrounding ectomycorrhizal roots.

mazaedium - a dry, powdery mass of meiospores and sterile elements with the ascomata of Caliciales and Onygenaceae.

medallion clamp - a clamp connection with hole or space between the hook and the hypha.

medulla - tissue beneath the outer layer (cortex) of an apothecium.

medullary excipulum (**-a**, pl.) - the central or inner non-hymenial tissue of an apothecium.

Melzer's reagent - a solution of iodine, IKI, and chloral hydrate.

merosporangium (**-a**, pl.) - a cylindrical sac containing a few sporangiospores in some zygomycetes.

metabasidium (**-ia**, pl.) - the portion of a basidium in which meiosis occurs.

metula (**-ae**, pl.) - a conidiophore branch having phialides, *e.g. Penicillium*.

micaceous - covered with glistening particles.

micronematous - conidiophore is similar to vegetative hyphae.

mitic system - the types of hyphae (generative, skeletal, binding) in the basidiocarps of the Aphyllophorales.

monokaryon - having genetically identical nuclei in the protoplast.

monomitic - having only one type of hyphae in the sporocarp.

mononematous - conidiophore of a single hypha, *cf.* synnematous.

monophyletic - a taxon or series of taxa composed of forms that have all descended from a recent and common ancestor; a single evolutionary lineage.

monoverticillate - having only phialides, *e.g. Penicillium*.

muriform - a type of spore with transverse and elongate internal walls.

mushroom - a general term usually applied to fleshy and conspicuous fruit bodies or those that are somewhat umbrella-shaped at least.

mycangium (-ia, pl.) - a specialized pocket in some insects that contains symbiotic fungi.

mycelium (-ia, pl.) - a mass of hyphae.

mycetismus - mushroom poisoning.

mycobiont - the fungal partner in a symbiosis.

mycocoenosis - the assemblage of fungi in an area or substrate.

mycolatry - the worship of fungi.

mycologist - someone who studies fungi.

mycoparasitism - one fungus parasitising another.

mycophagy - eating of fungi.

mycosis - fungal disease of humans and other vertebrates.

mycothallus - symbiosis with a fern and bryophyte gametophyte thallus.

mycotoxin - a toxin produced by a mold and released into the substrate.

mycotrophic - obtaining nutrients via mycorrhizal associations.

mycorrhiza (-as, pl.) - physical association between a root and a fungus.

necrotroph - an organism that derives its food from the dead cells of a living organism, *cf.* biotroph.

neoteny - reproductive competence in an otherwise juvenile form.

occluded - closed or filled in as in a hyphae in which secondary wall material compresses the protoplast.

octopolar - three loci control compatibility, *e.g. Psathyrella coprobia*.

odontoid - tooth-like or bearing teeth.

oenology - the study of wines and wine making.

oidium (-ia, pl.) - strictly speaking, a small spore that functions as a gamete.

onychomycosis - fungal degradation of toe- or fingernails.

operculum - the hinged lid on a sporangium (or ascus) that permits the release of ascospores.

ostiole - opening in apex of sac-like ascocarp or pycnidium.

outgroup - a taxon which is related to the ingroup taxa but does not share the same common ancestor as the ingroup; selected for phylogenetic analyses to give perspective to distance among taxa in an array. Selection of an outgroup can affect the interpretation of the relationship among the members of the ingroup, because something that is “way” out will make the cluster tighter than something that is phylogenetically closer.

paraphysis - sterile thread-like branched or unbranched hyphal element originating from the tissues underlying the asci and extending upward. In discomycetes, paraphyses often swell at the apex and form a layer (epithecium) over the asci.

parasexual cycle - genetic recombination occurs without meiosis in some fungi imperfecti.

parasite - an organism that extracts nutrients from another organism; may or may not cause disease.

parenthesome - cup-shaped enclosures on either side of the dolipore septum in basidiomycetes.

pectinolytic - able to degrade pectin via synthesis of pectinase.

pedicel - a small stalk.

peridiole - a component of the glebal tissues in some Gasteromycetes, especially the Nidulariales; surrounded by a wall and functioning as a dispersal unit.

perispore - a sheath surrounding the spore wall.

perithecium (-ia, pl.) - a flask-shaped ascocarp with an ostiole.

phialide - a cell with a fixed conidiogenous locus at the tip through which asexual spores are extruded in (basipetal) series.

photobiont - the algal component of a lichen, also called phycobiont.

phragmospore - a spore with two or more transverse septa.

phycobiont - the algal partner in a lichen.

phylloplane - pertaining to the surface of a leaf.

pileus - a cap or shelf-like structure that supports the hymenophore.

plectenchyma - a thick tissue formed by tightly interwoven hyphae.

pleomorphic - having two or more distinctive reproductive stages.

plesiomorphic - the ancestral state of a character.

podetium (**-ia**, pl.) - an erect usually columnar structure bearing one or more apothecia at its apex in some lichens.

prolate - elongated along the polar axis.

proteophilous fungi - sometimes called “ammonia fungi”; associated with urea-rich substrata.

prototunicate - asci which dissolve at maturity.

pseudofungi - the fungus-like protists and chromists, inlcuding oomyctes, hyphochytridiomycetes, and some other organisms.

pycnidium (**-ia**, pl.) - a sac-shaped structure in which conidia are formed.

pycnium (**-ia**, pl.) - a haploid structure in the life cycle of rust fungi resembling a pycnidium but producing pycniospores and receptive hyphae, enabling nuclear transfer and dikaryotization.

pyriform - pear-like in form

Q - a value given to asco or basidiospores reflecting the ratio of length to breadth; *e.g.* ellipsoidal or ovoid if < 2, oblong to fusoid if > 2. See also ubiquinone.

rachis - central axis of a feather or frond-like structure.

rachiform - a configuration of a conidiogenous structure in which the conidiogenous cell produces a conidium and then elongates in a “zigzag” pattern as more successive conidia adhere at the angles.

raduliform - a configuration of a conidiogenous structure in which the conidiogenous cell produces a conidium, elongates along the same axis and produces another conidium and so on, *cf.* rachiform.

ramicolous - on branches.

ramus (**-i**, pl.) - a cell bearing several smaller branches or phialides, as in the penicillia.

reniform - kidney-like in form.

resting spore - a spore that requires to withstands a period of quiescence (winter, drought, etc.) before germinating, *e.g.* teliospores and zygospores.

resupinate - lying flat against the surface of the substrate.

reticulate - net-like.

rhexolytic - release of a spore by dissolution or rupture of subtending cell or cells.

rhizine - root-like extensions from the undersurface of some lichens.

rhizomorph - root-like, coaxial aggregation of parallel vegetative hyphae.

rhizoplane - surface of a root.

rimose - cracked; usually following a radial pattern on a pileus or mycelium in culture.

rostrate - beaked.

r-selection - refers to the propensity of some species to be "weedy" so that they can colonize newly available substrata quickly, *i.e.* numerous spores, rapid growth rate, rapid cycling from spore to spore, etc.

rugose - wrinkled.

Saccardo spore groups - conidia are categorized based on morphological features such as shape, number of septa, and colour.

saprobe (= saprogen or saprotroph) - uses dead material as a source of carbon and energy.

saxicolous - growing on rock.

schizolytic - a type of spore secession arising from splits between the spore and its subtending cell(s).

sclerotium (**-ia**, pl.)- perennating structure composed of mycelium and sometimes host tissue; not containing or bearing spores.

scyphus - cup shaped apex of a podetium in some lichens, *e.g. Cladonia.*

secotioid - basidiomycetes in which the pileus does not expand. Hymenial tissues remain convoluted within the sporocarp and active basidiospore release is lost.

septal pore cap - a parenthesome; found associated with dolipore septa of basidiomycetes.

septum (**-a**, pl.) - a cross wall in a hypha.

sequestrate - a term describing sporocarps which do not open up to actively liberate their spores. *Rhizopogon* is a sequestrate member of the *Suillus* lineage.

sessile - a pileus or similar structure which lacks a stem.

seta (**-ae**, pl.) - a stiff, sterile hair, usually pigmented.

setose - possessing stiff hairs.

sibling species - a taxon (or taxa) which are genetically distinct (and reproductively isolated) from another taxon, but morphologically similar to the point of being almost indistinguishable.

soralium (**-ia**, pl.) - an area (crack or opening) on the surface of a lichen through which soredia are liberated.

soredium (**-ia**, pl.) - a vegetative propagule which is a loose conglomeration of hyphae and algal cells in lichens.

sorus (**-i**, pl.) - a discrete area from which spores arise in mass; usually describes sporogenous zones on the host plants infected with a rust or smut.

spalted wood - wood marked with zone lines of xylicolous fungi.

spawn - a friable material colonized by a pure culture of a fungus and used a source of inoculum, *e.g.* "mushroom spawn" is generally composed of grains inoculated with a variety of *Agaricus bisporus*. The infected grains are used to "sow" mushroom beds.

sphaerocyst - an inflated, globose cell in the tissues of some fleshy basidiomes of agaricoid fungi. Characteristic of the Russulaceae.

spindle pole body - an area on the nuclear membrane of fungi from which microtubules emanate during cell division.

spinulose - delicately spiny, also spinose.

sporangium (**-ia**, pl.) - an cell that differentiates within to form sexual or asexual spores.

sporangiolum (**-a**, pl.) - a small, few-spored sporangium in the zygomycetes.

sporangiophore - a cell that supports the sporangium.

sporangiospore - spore borne on a sporangiophore, *e.g.* zygomycetes.

sporeball - an aggregated cluster of teliospores and associated sterile cells in some smut fungi.

sporocarp - a general term for any spore-producing body.

sporocladium (**-ia**, pl.) - a spore bearing branch; used specifically in reference to the Kickxellaceae.

sporodochium (**-ia**, pl.) - a cushion-shaped body on which mitospores are produced.

squamulose - bearing small scales.

statismospore - a spore that is not forcibly ejected, *cf.* ballistospore.

sterigma (**-ta**, pl.) - the projection through which a basidiospore forms.

stichobasidium - a basidium in which the direction of nuclear division is parallel with the long axis of the basidium, *cf.* chiastobasidium.

stilbaceous - = synnematous.

stilboid - a propagule that resembles a mushroom.

stipe - stalk.

stroma (**-ta**, pl.) - a mass of vegetative hyphae (and sometimes host tissue) that gives rise internally or externally to spores.

stylospore - a sporangiolum, the "Stielgemmen" of Linnemann, *e.g. Mortierella*.

suaveolent - producing a sweet smell.

subiculum - a mycelial growth underlying the sporocarps of some fungi.

substrate - can be used in both a chemical (material on which enzymes are active, *e.g.* cellulose, lignin) and ecological sense (material on which something is growing, *e.g.* wood, bark, soil, etc.).

sulcate - bearing grooves.

sympodial - a pattern of spore production in which the terminus of sporogenous cell produces a spore and then below the spore produces a small branch which extends to produce another spore, etc.

synanamorph - one of two or more conidial states produced by a fungus.

synnema - many conidiogenous filaments forming an erect, compound sporophore with conidia.

systemic - throughout the host (if referring to an endophyte).

taxon - a taxonomic group of any rank.

terricolous - growing on the ground.

terverticillate - having branching at three levels, *i.e.* having rami bearing metulae and phialides, *e.g. Penicillium.*

thallic - refers to a type of conidiogenesis in which the spore arises directly from a segment of hypha after a septum forms.

tinea - a skin disease caused by a dermatophyte.

tomentose - covered with soft hairs.

trichogyne - a hair-like extension of the female gametogenous cell in some ascomycetes that receives the male gamete.

trimitic - a basidiocarp with three types of hyphae: generative, skeletal, and binding.

tip cell - the terminal cell of a hypha and site of elongation of the hypha.

tip growth - hyphal elongation is the result of extension of the tip of the hypha rather than any intercalary explansion.

trophocyst - the swollen base of a *Pilobolus* sporangiophore.

truncate - with an abrupt rather than rounded or blunt terminus.

truffle - the colloquial term for a hypogeous, ball-shaped sporocarp. Strictly speaking, the term refers to the ascocarps of the genus *Tuber*.

ubiquinone - terpenoid lipid that carries electrons; side chain length varies in number of isoprenoid units. Short form is "Q" followed by length of side chain, *e.g.* Q8, Q9, Q10, and sometimes by "H" to indicate if the chain is hydrogenated. Some taxonomic significance.

umbilicate - having a connecting cord or discrete, rounded, and shallow depression.

umbo - a central boss-like swelling.

uncinate - resembling a rounded hook.

unitunicate - an ascus with what appears to be a single wall layer.

vegetative (or somatic) incompatibility - a mechanism that prevents the fusion of hyphae of the same species.

velar - pertaining to the veil or veils of a mushroom.

verrucose - having small rounded processes, or warts.

verticillate - whorled, having parts, such as phialides, in rings, *e.g. Verticillium.*

vesiculate - made from or filled with vesicles.

viscid - slimy.

volutin - a polyphosphate storage material in yeasts and appearing as electron dense granules.

volva - the remains of the universal veil forming a cup-like base on the stipe of mushrooms.

warted - having a warty surface ornamentation.

white rot - wood decay in which the lignin is removed to leave the pale-coloured cellulosic residues. Often stringy in consistency.

Woronin body - a refractive, membrane bound organelle with crystalline contents (EM); associated with septa of many ascomycetes.

xanthochroic - tissue that turns dark with KOH, *e.g.* basidiocarp tissue of the Hymenochaetaceae.

xerophilic - having an affinity for very dry habitats.

yeast - a fungus consisting of mostly single cells that reproduce by budding or fission.

zearalenone - a mycotoxin that has hyperestrogenic effects in mammals.

zone lines - dark, sharply defined lines in wood that show the junction between vegetatively incompatible mycelia. Microscopically, the dark lines are made up of wood cells containing pseudosclerotia.

zoospore - a motile spore.

zoosporangium (**-ia**, pl.) - a cell producing motile spores.

zygospore - a resting cell produced by the zygomycetes; often heterokaryotic and formed preceding meiosis.

zygote - cell in which two compatible nuclei have fused.

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APPENDIX 6. *CURRICULUM VITAE*

Markus N. Thormann
Biological Sciences Department, CW-405
University of Alberta
Edmonton, AB, T6G 2E9, Canada

Education

2001 – **Ph.D.**, Environmental Biology and Ecology, Biological Sciences Department, University of Alberta, AB, Canada.

Thesis title: The fungal communities of decomposing plants in southern boreal peatlands of Alberta, Canada.

1995 – **M.Sc.**, Plant Biology, Botany Department, University of Alberta, AB, Canada.

Thesis title: Primary production and decomposition in wetlands of the boreal region of Alberta, Canada.

1992 – **B.A. (Min.)**, Geography, Queen's University, Kingston, ON, Canada.

1991 – **B.Sc. (H.)**, Biology, Queen's University, Kingston, ON, Canada.

Scholarships, Fellowships, and Other Awards

2000 – Biological Sciences Department award for Excellence in Teaching, University of Alberta
– Mary Louise Imry graduate student travel grant, University of Alberta
– Department of Biological Sciences graduate student travel grant, University of Alberta

1999 – Izaak Walton Killam Memorial Scholarship, University of Alberta
– Peggy Thompson Publication award for best publication in a refereed scientific journal, Alberta Society of Professional Biologists

1998 – Province of Alberta Fellowship, University of Alberta

1995 – Lakshmi Memorial Scholarship for Excellence in Teaching, University of Alberta

1994 – Province of Alberta Scholarship, University of Alberta
– University of Alberta award for Excellence in Teaching, University of Alberta

1987 – Proctor & Gamble Inc. Scholarship, Queen's University

Research Grants

1999 – Izaak Walton Killam Memorial Scholarship research grant, $1,500.00/two years, University of Alberta

1998 – Society of Wetland Scientists, $3,800.00/three years (renewed annually), University of Alberta

1977 – Challenge Grant in Biodiversity (Department of Biological Sciences, University of Alberta, and the Alberta Conservation Association), $13,900.00/two years, University of Alberta

1997 – Canadian Circumpolar Institute, $3,000.00/two years, University of Alberta

1994 – Canadian Circumpolar Institute, $4,800.00/two years, University of Alberta

Publications

Refereed publications

Vitt, D. H., L. A. Halsey, C. Campbell, S. E. Bayley, and **M. N. Thormann**. In press. Spatial patterning of net primary productivity in wetlands of continental western Canada. Écoscience.

Thormann, M. N., C. L. Myrholm, and K. I. Mallett. 2001c. *Armillaria sinapina* in herbaceous plant material from a peatland in Alberta, Canada. Canadian Journal of Botany **79**: 643-647.

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Campbell, C., D. H. Vitt, L. A. Halsey, I. D. Campbell, **M. N. Thormann**, and S. E. Bayley. 2000a. Net primary production and standing biomass in northern continental wetlands. Northern Forestry Centre, Natural Resources Canada, Canadian Forest Service, Edmonton, AB, Canada. Information Report NOR-X-369.

Thormann, M. N., Currah, R. S., and S. E. Bayley. 1999b. The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta, Canada. Wetlands **19**: 438-450.

Thormann, M. N., A. R. Szumigalski, and S. E. Bayley. 1999a. Peat accumulation potentials of peatlands in southern boreal Alberta, Canada. Wetlands **19**: 305-317.

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Thormann, M. N. and S. E. Bayley. 1997d. Response of net aboveground primary plant production to nitrogen and phosphorus fertilization in peatlands in southern boreal Alberta, Canada. Wetlands **17**: 502-513.

Thormann, M. N. and S. E. Bayley. 1997c. Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. Plant Ecology **131**: 1-16.

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Thormann, M. N. and S. E. Bayley. 1997a. Decomposition along a moderate-rich fen - marsh peatland gradient in boreal Alberta, Canada. Wetlands **17**: 123-137.

Non-refereed publications

Thormann, M. N. and D. A. Locky. In press. Wetlands - taking the mystery out of these mysterious ecosystems. IRIS, Newsletter of the Alberta Native Plant Council, Edmonton, AB, Canada.

Vitt, D. H., L. A. Halsey, and **M. N. Thormann**. 1997. The wetlands of Alberta: A 1:1,000,000 summary map, 2nd Edition with revisions. Alberta Environmental Protection Agency, Edmonton, AB, Canada.

Vitt, D. H., L. A. Halsey, **M. N. Thormann**, and T. Martin. 1996. Overview of peatland resources in the natural regions and subregions of Alberta. Alberta Peatland Resource Centre, Edmonton, AB, Canada. Publication 96-1.

Bayley, S. E., F. Bishay, B. Donahue, M. Hrudka, E. Jenkins, R. Madro, L. Maslin, R. Mewhort, C. Smyth, M. Spafford, **M. N. Thormann**, J. White, H. Wind-Mulder, and S. Urban. 1995. Feasibility of using a restored wetland in Stettler Alberta to provide tertiary treatment of municipal wastewater. Report to Ducks Unlimited, Edmonton, AB, Canada.

Conference Abstracts

Thormann, M. N., S. E. Bayley, and R. S. Currah. 2001. "Effects of temperature on decomposition rates of the dominant vegetation of southern boreal peatlands by bacteria and fungi", Canadian Botanical Association, Kelowna, B.C., Canada.

Thormann, M. N., S. E. Bayley, and R. S. Currah. 2000. "Decomposition rates of above and below ground tissues of the dominant vegetation in boreal peatlands", Society of Wetland Scientists 21st annual meeting, Quebec City, PQ, Canada.

Piercey, M. M., **M. N. Thormann**, and R. S. Currah. 2000. "Mycorrhizal endophytes of members of the Ericaceae can form mycorrhizas with *Picea mariana in vitro*", 34th Prairie Universities Biological Symposium, Regina, SK, Canada.

Thormann, M. N., R. S. Currah, and S. E. Bayley. 1999. "Some interesting fungi isolated from living and decomposing *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada", Society of Wetland Scientists 20th annual meeting, Norfolk, VA, U.S.A.

Mewhort, R., **M. N. Thormann**, and S. E. Bayley. 1998. "Ecological processes in wetlands across a gradient of boreal wetlands", North American Lake Management Society, 18th International Symposium, Banff, AB, Canada

Thormann, M. N., S. E. Bayley, and R. S. Currah. 1998. "The mycorrhizal status of the dominant vegetation along a bog – fen - marsh peatland gradient in southern boreal Alberta, Canada", Canadian Botanical Association, Saskatoon, SK, Canada.

Teaching Experience

Teaching development

1998 – Attended University Teaching Workshop seminars

1994 – Peer Councilor for Botany 199 Teaching Assistants and Demonstrators

– Attended University Teaching Workshop seminars

– Read "*Teaching Resource Manual*" (Neath, 1993), "*Teaching College Freshmen*" (Erikson and Strommer, 1991), and "*Teaching Assistant Strategies*" (Allen and Rueter, 1990)

– Watched "*Key Teaching Behavious in Post-Secondary Education: Exemplars of Effective Teaching*" video

1993 – Attended the "Teaching Assistant Peer Training" workshop for Botany 199

– Attended University Teaching Workshop seminars

Lectures

2001 – "*The basidiomycetes*", Botany 306 (Introductory Mycology), Dr. R. S. Currah (instructor)

– "*The agarics*", Botany 306 (Introductory Mycology), Dr. R. S. Currah (instructor)

2000 – "*Chytridiomycetes and zygomycetes*", Botany 201 (The Simple Eukaryotes: Algae, Fungi, and Lichens), Dr. R. S. Currah (instructor)

– "*Fungi in ecosystems: nitrogen, phosphorus, and carbon cycling*" Botany 306 (Introductory Mycology), Dr. R. S. Currah (instructor)

1999 – "*Fungi in ecosystems: nitrogen and phosphorus cycling*", Botany 306 (Introductory Mycology), Dr. R. S. Currah (instructor)

– "*Fungi and algae in wetlands*", Botany 201 (The Simple Eukaryotes: Algae, Fungi, and Lichens), Dr. R. S. Currah (instructor)

– "*Genes and proteins*", Biology 107 (Introduction to Cell Biology), Dr. T. Lumley (instructor)

1998 – "*Global climate change and its effect on wetlands*", Earth and Atmospheric Sciences 205 (Environment Earth), Dr. C. Campbell (instructor)

– "*Fungi in ecosystems: nutrient cycling aspects*", Botany 306 (Introductory Mycology), Dr. R. S. Currah (instructor)

– "*Are Alberta's peatlands endangered?*", Botany 384 (Global Change and Ecosystems), Dr. S. E. Bayley (instructor)

– "*Peatlands in Alberta - past, present, and future perspectives*", Earth and Atmospheric Sciences 205 (Environment Earth), Dr. C. Campbell (instructor)

1997 – "*The nitrogen cycle in aquatic ecosystems*", Zoology 464 (Limnology), Dr. K. Devito (instructor)

1996 – "*An overview of factors that influence peatland development in Canada*", Botany 304 (Field Botany), Dr. D. Archambault (instructor)

1995 – "*Production and decomposition in a bog – fen - marsh wetland gradient in central Alberta, Canada*", Zoology 664 (Limnology and Fisheries), Dr. E. Prepas (instructor)

Laboratory Instruction

1998 – Botany 201, "The Simple Eukaryotes: Algae, Fungi, and Lichens"

– Biology 315, "The History of Biology"

1997 – Biology 108, "Organisms in their Environment"

1996 – Biology 208, "Principles of Ecology"

1995 – Botany 199, "Introductory Botany"
    – Peer councilor for Botany 199 Teaching Assistants and Demonstrators
1994 – Botany 199, "Introductory Botany"
    – Botany 130, "Ecology for Forestry Students"
1993 – Botany 199, "Introductory Botany"
    – Botany 130, "Ecology for Forestry Students"

Professional Employment

1995 – 1996 Biophysical Research Technician, Dr. D. H. Vitt, University of Alberta, AB
Responsibilities – air photo interpretation for wetlands in Alberta and Saskatchewan, data management, statistical data analyses, writing of reports, laboratory/field work

Professional Affiliations

- *American Bryological and Lichenological Society* (2000-present)
- *Alberta Native Plant Council* (1997-present)
- *Alberta Society of Professional Biologists* (1997-present)
- *Society of Wetland Scientists* (1997-present)
- *Edmonton Mycological Society* (1997-present, Treasurer and Membership Director, 1997-2001)

Additional Academic Achievements and Endeavors

- Reviewer of submissions for publications in *Mycological Research*, *Canadian Journal of Botany*, *American Journal of Botany*, and *Wetlands*
- Organization of a Discussion Group for students interested in Mycology
- Mentor to graduate students
- Representative of the Organization of Botany Students to the Graduate Student Association, University of Alberta
- Graduate Student representative to the Graduate Student Admission Committee, University of Alberta
- Assisted with revisions of the Botany 130 laboratory manual